XIV. *On the Comparative Structure of the Brain in Rodents.*

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[PLATES 49, 50.]

IN a former memoir published in the Philosophical Transactions* I have detailed the result of researches into the minute anatomy of the cortex cerebri in the Pig as contrasted with that of the Sheep, the Cat, and other animals. In continuation of the same series of researches it is proposed to consider here the results obtained by a still more extended enquiry into the structure of the brain in the Rodentia, and with this object in view, I shall divide my subject into the two lines of investigation followed out:—first, *the histology of the entire cortical envelope*, and secondly, *the central projections of the olfactory organ.* It is necessary that such an account be preceded by a short sketch of the external conformation of the brain in Rodents, and that its topography should be mapped out under the more recent and accurate nomenclature introduced by the late Professor BROCA, whose work upon the comparative anatomy of the convolutions in Mammalian brains† is by far the most philosophical and trustworthy treatise which has appeared on this subject since the publications of TURNER,‡ BISCHOFF,§ and ECKER.‖ Since the cerebrum of the Rabbit affords the type for the brain of the Rodent, and since this animal, together with the Rat, was chiefly utilised in these investigations, my sketch will be limited to the brains of these two animals.

EXTERNAL CONFORMATION OF BRAIN IN THE RAT AND RABBIT.

When investigating the structure of the brain in the Pig and Sheep I had to deal with a highly developed olfactory apparatus, associated with a richly convoluted

* "Researches on the Comparative Structure of the Cortex Cerebri," Phil. Trans., Part I., 1880.

† "Anatomie Comparée des Circonvolutions," par M. PAUL BROCA. Revue d'Anthropologie.

‡ "Convolutions of the Human Cerebrum Topographically considered." W. TURNER, Edin. Med. Journ., 1866.

§ "Die Grosshirnwindungen des Menschen." Dr. Th. L. W. BISCHOFF. München, 1868.

‖ "The Convolutions of the Human Brain." Dr. ALEX. ECKER. Translated by J. C. GALTON.

cortex. In the brain of the small Rodents now under consideration there is also a notable development of the olfactory organ and its central connexions, but on the other hand the great extra limbic or parietal mass is wholly devoid of gyri. The Mammals possessing such smooth, non-convoluted brains have been grouped in an artificial class by OWEN, who terms them *Lissencéphales;* the animals possessing convoluted brains are termed *Gyrencéphales.* BROCA, on the other hand, has adopted the terms Osmatic* and Anosmatic Mammals,† as indicative of a highly-developed olfactory apparatus in the one, as contrasted with the defective, rudimentary, or wholly absent olfactory lobes of the other class. Both these terms are extremely useful in such investigations as we at present are concerned with, and I shall therefore freely adopt them, together with the nomenclature of the convolutions advocated by BROCA. From what has been stated it is obvious that Osmatic Mammals may have smooth or convoluted brains, but the Rat and Rabbit present us with typical brains of the Osmatic Lissencéphales. The cerebrum in these animals is mapped out into two grand divisions :—

1. A median portion, encircling the basal ganglia and peduncular mass as it leaves the cerebrum, forming the great limbic lobe.
2. The more exposed hemispheric mass forming the outer and upper aspect of the brain corresponding to the parietal lobe of higher animals, and which I shall term, after BROCA, the extra-limbic mass.

The former, or great limbic lobe, is divisible into three portions—

a. An upper arc corresponding to what has been called the convolution of the corpus callosum (gyrus fornicatus).
b. A lower arc, also called the gyrus hippocampi.
c. An anterior arc, formed by the olfactory lobe, which unites the upper and lower limbic arcs.

Looked at from above, the brain of the Rat is heart-shaped, with the apex directed forwards. The hemispheres diverging behind reveal a minute, semi-translucent, pale-grey body, ovoid in form, projecting betwixt them, the pineal body, posterior to which the corpora quadrigemina appear. The surface of the extra-limbic mass is almost perfectly smooth, being marked only by a few extremely delicate venules. There is no distinct frontal, occipital, or temporal lobe differentiated from this extra-limbic mass, which must be regarded as entirely constituting a parietal lobe. We therefore find no trace of a fissure of ROLANDO, as is distinctly seen in Osmatic Gyrencéphales (*e.g.*, Pig and Sheep).‡ We shall, however, retain the terms frontal and occipital

* Includes the large majority of Mammalian brains.

† The Cetacea, Amphibious Carnivora, and Primates.

‡ Vide Plate 9, fig. 2, *op. cit.*

poles, as indicative of the anterior and posterior extremity of the hemisphere, it being understood that these terms do not imply the existence of a frontal or occipital lobe. The inner margin of the hemispheres bordering upon the great longitudinal fissure may also be conveniently spoken of as the sagittal border. Along this border, in the hinder half of the hemisphere, there is seen a strip of cortex, much paler than the remaining portion of the hemisphere, about 2 mm. wide behind, but becoming gradually narrower as it extends forwards. This pale strip is not marked off by any linear depression, yet it forms an important region characterised by a peculiar type of cortex. In the Rabbit, on the other hand, the same sagittal region is mapped off from the extra-limbic mass outside it by a constant though shallow depression (Plate 49, fig. 1, K K), the representative of the primary parietal sulcus of higher animals, and which, as in the Pig and Sheep, separates the sagittal from the Sylvian gyri of the parietal lobe. Moreover, the upper aspect of the brain in the Rabbit is of more pyriform contour, and remarkably attenuated in front, so that the pointed frontal poles contrast strangely with the broader frontal extremities of certain animals included in the same category (fig. 8, Beaver, *op. cit.*, Broca.). The hemispheres of a four-months' old Rabbit measured 28 mm. long, and weighed (together with corpora quadrigemina) just six grammes. The extra-limbic lobe is traversed by three or four delicate channels for blood-vessels, which course upwards and backwards from the limbic fissure, and very slightly indent its surface. At the widest portion the cerebrum has a diameter of 30 mm., whilst in the Rat it is but 15 mm. across. The brain of the Rat displays the same cordate outline at its base, the hemispheres widely separated behind by the descent of the cerebral peduncles. The lower limbic arc forms so prominent a feature as *wholly to conceal from view* the lateral portions of the extra-limbic lobe (Plate 49, fig. 2, N). The base of this cordate area is therefore formed by the gyrus hippocampi, in front of which extends the olfactory lobe. Along the course of each olfactory lobe the superficial olfactory medulla (external root) runs back, rapidly narrowing as it approaches the gyrus hippocampi, in which it loses itself (Plate 49, fig. 2, M). Betwixt the two superficial olfactory bands, and in front of the optic commissure, lie two pyriform grey areas, the olfactory field of Gratiolet (Plate 49, fig. 2, P). They are bounded externally by the fasciculus just named, and lie in contact with one another on the inner side, the optic nerves being here placed superficial to them. The optic nerves terminate in a well-marked optic commissure (Plate 49, fig. 2, R), from which the optic tracts diverge, and are lost beneath the gyrus hippocampi. The tuber cinerum and infundibulum forms a prominent mass of grey matter behind the optic commissure (Plate 49, fig. 2, L), and are crossed behind the optic tracts by a distinct white band of fibres extending across the angular interval left betwixt the diverging tracts. Stellate pigment cells of a jet-black hue accumulate more or less thickly along the whole lower limbic arc and olfactory lobe. They are especially frequent over the basal aspect of the olfactory lobe and along the limbic fissure, back even as far as the posterior extremity of the latter.

Upon separating the olfactory lobe from the frontal end of the hemisphere and reflecting it backwards, we become aware of the fact that the frontal extremity is obliquely truncated, sweeping forwards and upwards to the frontal pole, and thus forming an oblique depression in which lies the opposed olfactory lobe. Into this part of the hemisphere runs the upper or fourth olfactory fasciculus. If we direct our attention to the base of the brain in the Rabbit, on the other hand, we observe that the great limbic lobe does not, as in the Rat, conceal by its extension outwards the extra-limbic portion of the hemisphere, a large portion of which projects on either side of the well-marked limbic fissure. The olfactory lobe runs directly forwards beneath the frontal extremity of the hemisphere, its external or superficial fasciculus coursing backwards parallel to, and 2 mm. distant from, the limbic fissure (Plate 49, fig. 1, M), until at the gyrus hippocampi it curves inwards and is lost to view. On the median aspect of the Rabbit's brain the upper limbic arc is deep anteriorly, but narrowed behind, and curving down behind the corpus callosum, forms a deep fossa, here overlapped by the occipital pole in which lies the quadrigeminal bodies. Below this it becomes continuous with the gyrus hippocampi or lower limbic arc (Plate 49, fig. 1, B). Along the upper arc two delicate furrows are seen, the representatives of the sub-frontal and sub-parietal segments of the limbic fissure (Plate 49, fig. 1, A). In the Rat, however, there is no trace of any such furrows, the upper arc being here directly continuous with the sagittal portion of the parietal lobe. In both animals the Sylvian fissure is nearly absent, being indicated by a very slight depression betwixt the gyrus hippocampi and the olfactory region (Plate 49, figs. 1, 2, S).

Section I.—The Cerebral Cortex.

The complete cortical envelope of the cerebral hemispheres in the animals under consideration (and this with special application to the Rabbit and the Rat) may be readily mapped out into six distinct regions characterised by a notable diversity in their laminar constitution (Plate 49, fig. 1). These regions, abruptly marked off from each other by their topographical relationships as well as their intimate structure, are the upper limbic arc, the lower and anterior limbic arcs, the extra-limbic lobe, the olfactory bulb, and the cornu ammonis; but whereas the two former of these regions are subject to further modifications of their textural laminations—modifications which are not simply those of *degree*, but of *kind*—it results that I must extend my classification of the varied cortical realms beyond the limits mapped out by former authorities. Thus Meynert distinguishes five *types* of cortical lamination as follows :—

1. A common type.
2. Occipital type.
3. Sylvian type.
4. Type of cornu ammonis.
5. Type of olfactory bulb.

He also casually refers to a peculiar constitution of the olfactory area, but enters into no detailed account of the same, stating that it still awaits a monographical exposition.*

Since, in accordance with the rule which I find it essential to adopt as to what is to be understood by a divergence in the *laminar type* of the cortex, I should exclude from his list the third or Sylvian, the diversities of structural type embraced in MEYNERT'S category will be four only. This, however, but very inadequately expresses the truth as regards the cortex of the Mammalian brain, for I find at least *eight characteristic cortical areas* distinguished by their laminar structure. These we may enumerate as follows :—

1. Type of upper limbic arc.
2. Modified upper limbic type.
3. Outer olfactory type.
4. Inner olfactory type. } Comprised within the limits of the lower and
5. Modified olfactory type. } anterior limbic arcs.
6. Extra-limbic type.
7. Type of cornu ammonis.
8. Type of olfactory bulb.

In enumerating these types I have distinguished them by terms having special reference to their regional distribution, not that I believe this to be the better method ultimately to adopt, but the simplest in our present state of defective knowledge upon these points. With advancing knowledge of the intimate structure and peculiarities of the various regions of the cerebral cortex it will be found advisable to term these varied types after some important and essential structural peculiarity. The same remark applies to the enumeration of the individual cortical layers which are usually denominated by their relative positions as first, second, or third layers, &c. This method cannot fail to mislead and introduce much confusion, since we are constantly meeting with intercalation of fresh layers or the absence of others, and as a result of this method the same denomination becomes applied to layers which are wholly different in constitution. It is, therefore, on this account necessary to term each layer after some characteristic structural feature, more especially one which finds its counterpart in all the various members of the Mammalian series, and to subordinate the numbering of layers to the expression of their relative depth.

Upper Limbic Arc (Plate 49, fig. 1).

Adopting the above considerations, I find it necessary to regard the cortex typical of the upper limbic arc as consisting of four well differentiated layers, which may be termed respectively—

* "The Brain of Mammals," STRICKER'S 'Human and Comp. Histology,' Sydenham Soc. Trans., vol. 2, p. 414.

1. Peripheral cortical zone.
2. Small pyramidal layer.
3. Ganglionic layer.
4. Spindle cell layer.

1. *Peripheral cortical zone.*—As seen by the naked eye this is a uniformly light grey belt sharply defined from the darker layers beneath. Its structure, revealed by microscopic aid, does not differ from that of higher animals, being constituted of a fine neuroglia matrix derived from the delicate prolongations of connective cells supporting the meshwork formed by the repeated sub-divisions of the apical processes of nerve-cells in the underlying strata. We meet here, as in the Sheep, Pig, and other animals, with the DEITER cell. These cells are found immediately beneath the pia-mater, their processes extending downwards into this layer and *a larger process invariably being connected* with a nucleus along the sheath of a blood-vessel. As regards depth there is a very evident diminution of this layer upwards and outwards over the exposed aspect of the hemisphere as well as backwards towards the occipital pole. Thus in regions of this upper limbic arc anterior to the corpus callosum the depth is ·511 mm., whilst posterior to this commissure it scarcely attains to ·377 mm. A still more notable diminution in depth occurs outwards, viz.: in extra-limbic regions where this outer cortical zone measures but ·279 mm. in depth. In the cortex of the Pig's brain a similar fact was noted and is recorded in the table of depths of the cortical layers given in my former paper.*

2. *Small pyramidal layer.*—In the upper limbic arc of the brain of Man and of some of the higher Mammalia I have described the typical formation as that of a five-laminated cortex. In the same region, however, of the Rabbit's brain the cortex is four-laminated, and this arises from the absence of the small oval and angular elements which in Man constitute the second layer. In certain localities, more especially extra-limbic in position, a shadowing forth of this stratum is represented by the closer aggregation of elements superficially which become also appressed in small clumps at intervals and may possibly represent a rudimentary form of this layer. So little marked is this in the upper limbic arc that it may virtually be considered devoid of this layer. The second layer, then, is in this region constituted by a stratum of small pyramidal nerve-cells as well as a few scattered angular cells. In the size of these elements, in their mode of distribution, in the depth of the stratum and its relationship to subjacent layers a very close resemblance is borne to the upper half of the third layer of higher animals. In the pyramidal cells of the human cortex a notable increase in their dimensions occurs with their depth so that at the lowest level of this series in Man I find cells whose proportions, though not usually so great as the cells of the still lower ganglionic layer, still render them giants beside their pigmy representatives higher up. This increase in size is *gradually* attained.† Now this feature is wholly absent in the small

* *Op. cit.*, p. 62.

† "The Cortical Lamination of the Motor Area of the Brain." Proceedings Roy. Soc., No. 185, 1878.

pyramidal layer of the Rabbit—the cells remain small to their lowest level. In form, these cells are usually pyramidal or pyriform, whilst the small irregular, angular cell is met with chiefly on the outskirts of this layer where it joins the outer cortical zone. The apex process of these cells divides and subdivides into a delicate network of fibrils, those which are deeper seated undergoing the primary division at some distance from the cell, those nearer the cortical zone undergoing instant division, so that instead of a single elongated apex process the apex of the cell itself is bifid or horned. A similar feature pertains to the subjacent layer, the apex process of which may be traced often into the outer cortical zone ere primary division occurs. It therefore appears probable that whilst the greater bulk of nerve-fibre element of the lower four or five layers is formed by the numerous secondary processes of the nerve-cell,* the outer cortical zone derives its nervous element chiefly from the apex process of cells of underlying strata. The fact that the bifurcate or horned cell is met with at the commencement of this layer in sparse detached clumps has been alluded to above as significant probably of a rudimentary form of the second layer of higher animals. Now it has been shown that this latter stratum is also extremely defective and in great part entirely absent in the cortex of the Sheep; in the Pig it is also but a shallow belt averaging ·093 mm. deep, increasing in certain regions to ·139 mm., or even ·186 mm., whilst in Man its greatest development is fully ·279 mm. in depth. It appears clear, therefore, that the development of this belt bears an important relation to the position of the animal in the scale of organisation. The average size of these small pyramids in the Rabbit is 13μ long by 9μ broad, with a nucleus of 8μ in length—the largest do not exceed $17\mu \times 12\mu$. This closely approximates to the upper series of the third layer in Man, which in the ascending frontal gyrus measure $12\mu \times 8\mu$, and in the ascending parietal gyrus $15\mu \times 11\mu$.

This second layer attains its greatest depth in that portion of the upper limbic arc lying in front of the corpus callosum, gradually diminishing in depth backwards, so that behind the corpus callosum it is but ·372 mm. as contrasted with ·883 mm., the depth of the anterior region. In the direction of the extra-limbic mass, *i.e.*, over the exposed aspect of the hemisphere, the depth of this layer is often increased to 1·023 mm., being double the depth in the limbic lobe on a corresponding plane.

3. *Ganglionic layer.*—Immediately beneath the small pyramids of the second layer at the frontal end of this upper arc we find the far larger cells of the ganglionic layer. These cells, whilst differing widely from those of the ganglionic layer in Man, approximate to them sufficiently in many features to justify us in regarding them as representatives of the same series. Thus they are the largest and most characteristic cells in the cortex; they lie immediately upon the spindle layer, with a slight pale poorly-celled zone extending above and below it as in Man; their processes are peculiarly elongated, extending right through the pyramidal series into the outer

* By secondary processes are meant all extensions from the cell exclusive of the apex and basal or axis cylinder process.

cortical zone; and lastly, with the increase from a four to a five-laminated cortex by the addition of a small angular layer, the latter lies immediately between the pyramidal layer and this stratum of large cells, which I therefore propose to consider as identical with the ganglionic series in Man. This intercalation of an angular layer between them and the pyramids suffices to distinguish them from the large pyramids of the lower half of the third layer in human brain. Another character common to this series and that of Man and higher animals is their distribution in confluent clusters, as a deep stratum on the one hand, or on the other, as the solitary or linear arrangement.* The confluent and linear arrangement of these elements is as marked a feature here as it is in the Pig and Sheep. It has been noted that the great development of the ganglionic series in Man was found associated with the five-laminated, and not the six-laminated, cortex, and was peculiarly distributed over the upper limbic arc in its anterior half—so in the Rabbit these cells vastly predominate in the four-laminated cortex, *i.e.*, before the intercalation of an angular layer occurs, and is richly distributed over the upper limbic arc and its immediate neighbourhood. To sum up the special features whereby I identify this layer with the common ganglionic series:—

a. The large size and characteristic form of the cells.
b. The histological structure of the stratum.
c. Peculiar distribution of apex processes.
d. Relationship to the angular layer.
e. Arrangement in dense clusters or solitary cells.
f. Special development in certain areas.

It now remains to consider how they differ histologically from the same series in higher animals, and this object will be best furthered by considering in detail the general structure of the ganglionic layer as regards—1, depth; 2, form of cell; 3, size of cell.

1. *Depth of ganglionic layer.*—Great variations in depth occur throughout this layer, corresponding to a more or less rich development of cells. Upon examining sections taken vertically through the hemisphere, as at B (Plate 49, fig. 3), one cannot fail to have the attention arrested by the rich development of these cells in the upper limbic arc, and their rapid diminution and thinning out in the outer regions of the extra limbic mass. Referring to our figure of the upper limbic arc in the Rabbit (Plate 49, fig. 3), let us briefly examine the depth of this layer along the length of this arc, as also along the upper angle where it unites with the extra limbic portion. The depth attained is as follows:—

* "The Comparative Structure of the Cortex Cerebri." BEVAN LEWIS. Phil. Trans., Part I., 1880, page 38.

	Limbic lobe. mm.	Union with extra-limbic. mm.
At A. (Plate 49, fig. 3) . .	·376–·418	·743
B. „ . .	·511	·743
C. „ . .	·232	·511
D. „ . .	·232	·372
E. „ . .	·279	·376

Hence its depth is greatest at A and B, increasing upwards and outwards towards the extra-limbic portion, and thus forming a specially rich formation in FERRIER's region (7).* When these measurements are contrased with those of the same stratum in the Pig,† a great similarity is at once perceived. As before shown, the depth varies with the two kinds of arrangement observed by these cells, viz. : the clustered or the solitary. Thus in the Pig the clustered cells attained an average depth of ·595 mm., whilst the dense confluent series in the Rabbit average ·506 mm. The depth, however, affords but an imperfect guide to the relative richness of the stratum in cells—a better notion is gained by the fact that the quarter-inch field will reveal in the confluent series as many as 90 to 100 cells, whilst the laminar series will give to the same power not over 6 or 8 cells.

2. *Form of cell.*—The cell of this series is usually an elongate pyramid, although the oval and large fusiform cell is occasionally met with, as is also a bifurcate or horned cell; the latter, however, far less common than in the Sheep and Pig. It was stated as regards the form of these cells in the Pig, a striking uniformity in their contour was observable, "by far the greater proportion taking the form of an elongate pyramid, the few exceptions occurring being usually gigantic spindles." ‡ In this respect the ganglionic cells in the Rabbit's brain agree with those of the Pig and Sheep in not exhibiting the great irregularity in marginal conformation, which is a peculiar character of the same series of cells in Man. The group of ganglionic cells from the cortex of the Pig, figured in my last memoir, represents the typical form here.§

3. *Size of cell.*—The dimensions attained by these cells along this region from before backwards have a fair uniformity. The largest cells are found at C and D (Plate 49, fig. 3), where they measure 32μ long by 18μ broad, having a nucleus 13μ in length. Anterior to this they measure $24\mu \times 17\mu$, whilst posterior to it they diminish gradually in size to $26\mu \times 16\mu$ behind the corpus callosum. With the exception of these slight variations I may state that throughout the upper limbic arc *great uniformity in the size of the structural elements of this layer is maintained.* When examining the structure of the parietal or extra limbic portion of the hemisphere we shall find still larger cells,

* Vide fig. 36, area 7, in brain of Rabbit. "The Functions of the Brain."

† *Op. cit.*, p. 62.

‡ *Op. cit.*, plate 7.

§ *Op. cit.*, page 43.

although they do not approach the dimensions of the same elements in the Pig. Thus in the upper limbic arc of the Pig the larger cells averaged $48\mu \times 17\mu$, the largest in the Rabbit being $32\mu \times 18\mu$, measurements suggestive not only of the greater size of these cells in the Pig, but of their far more *elongate* contour. The typically elongate cell however occurred in the Sheep, as exhibited by their measurements of $46\mu \times 11\mu$.

The above considerations lead us to conclude that whilst these cells undoubtedly represent the ganglionic series of Man and the higher Mammalia, yet in size, contour, and structural type these cells in the Rabbit lose the strong distinctive features which characterise the ganglion cells of Man, whilst on the other hand they acquire structural affinities to the *larger pyramids* in the human cortex approximating as closely to them as was the case in the Sheep and Pig; in short, the structural type of the ganglionic cell is modified, being less complex.

Regional distribution (Plate 49, fig. 3).—In describing the cortex of the Pig and Sheep it was shown that this ganglionic layer assumed the form of a nested or clustered and a laminar or linear arrangement of its cells, but that in the former case the clusters were either far apart or discrete, or tended to become confluent. In the Rabbit the true nested arrangement is not to be found, as the clusters all tend to become confluent. The characteristic formation therefore over the upper limbic arc is that of a deep and dense layer, the cells uniformly distributed throughout, and in this plan again they more closely resemble the large pyramidal cells of Man than the subjacent layer. In the portion of the upper limbic arc which bends down in front of the corpus callosum (Plate 49, fig. 3, A and B), there is a most notable development of this layer. The ganglionic belt is here deep, and consists of large cells densely congregated and commencing abruptly beneath the small pyramidal layer. Its depth and richness in cells increases upwards towards the *exposed aspect* of the hemisphere, the quarter-inch field usually showing 60 to 80 cells, so that the margin of the longitudinal fissure here has a most exceptionally rich development of this layer. This rich formation is continued outwards *over the whole of the areas numbered* 7 *and* 9 *by* FERRIER,* and terminates only at the limbic fissure. As in the corresponding series in higher animals, the deepest portion of this layer is pale, having very few small cells, although at wide intervals apart are found some of the largest size ganglionic cells. Again referring to the diagram, we find from C to D the decreasing depth of the layer shows a corresponding diminution in the richness of its cells, which, however, are still numerous as far as D, and increase in number toward the outer or exposed aspect of the hemisphere. Beyond the sagittal margin, however, we find that from being closely congregated, the poorest development of cells yet met with occurs, as they rapidly thin out into an almost linear series down the outer aspect of the hemisphere as far as the great limbic fissure. Betwixt them and the small pyramidal layer I met with a belt of small angular cells, so that the cortex becomes five-laminated. Beyond D, the layer becomes rapidly shallower and the cells distant

* "Functions of the Brain," fig. 36.

and sparse, 18 to 20 cells alone being seen in the quarter-inch field in striking contrast to their abundance in the areas A and B.

Continuing to diminish in depth and in the number of its cells, this layer becomes a very insignificant tract beyond E, being, however, always most richly developed along the sagittal angle of the hemisphere. The whole exposed or extra-limbic aspect of the hemisphere, from D to E, is distinctly five-laminated, and a typical linear arrangement of cells is maintained in the ganglionic layer—the cells being placed at wide distances apart, and all on the same plane or at a uniform depth from the surface of the cortex.

Modified Upper Limbic Type (Plate 50, fig. 4).*

It has been already inferred that the structural type of the *posterior extremity* of both upper and lower limbic arcs exhibit very important modifications. The change, as far as it affects the upper limbic arc, is as follows:—On the outer aspect of the hemisphere a shallow sulcus is seen (Plate 49, fig. 1, K) disposed parallel to the great longitudinal fissure and mapping off from the extra-limbic mass outside it, a portion of the hemisphere which in the convoluted brains of higher animals corresponds to the superior parietal or sagittal convolutions.

Now this sulcus forms an *abrupt boundary* betwixt two forms of lamination; external to it lies the cortex typical of the larger mass of the extra-limbic lobe, internal to it is a cortex distinguished by a remarkable granule formation. It has been noted that as we examine the upper limbic cortex towards the posterior extremity of the callosal commissure an intercalated series of granule and angular elements becomes interposed betwixt the small pyramidal and ganglionic layers (vide Plate 50, fig. 4). Now, these small angular cells increase rapidly in number, and approaching the surface wholly replace the second or small pyramidal layer. In lieu of the latter, therefore, we eventually find here a deep belt of densely congregated small granule-like bodies, the granule-like character being due to the large size of their nucleus compared with their investing protoplasm. They are very closely crowded at the upper limits of the layer, but less so at deeper levels, taking a position in horizontal serried rank which is an especial feature of this formation—a peculiarity due to their separation into rows by the passage betwixt them of arciform fasciculi or bundles of medullated fibres running parallel to the surface of the cortex. In this region, therefore, the cortex is still four-laminated, consisting of—

1. Outer cortical zone (Plate 50, fig. 4, A).
2. Deep belt of granule-like cells (Plate 50, fig. 4, B).
3. Ganglionic belt (Plate 50, fig. 4, C).
4. Spindle-cell layer (Plate 50, fig. 4, D).

This formation is not limited to the upper limbic arc, but stretching over on to the

* The area covered by this formation is shaded by dots in Plate 49, figs. 1 and 3.

exposed aspect of the hemisphere, extends to the shallow parietal sulcus above described (Plate 49, fig. 1, K). If we follow this formation backwards it is found to occupy the whole remaining median aspect of the hemisphere as far back as the limbic sulcus.* From this point downwards its distribution is more and more restricted to the inner moiety of the limbic lobe until it finally dwindles into an insignificant tract to disappear at the posterior extremity of the gyrus hippocampi. The gradually narrowing tract as it comes downwards and inwards leaves an angular portion of cortex betwixt it and the limbic sulcus, whose apex corresponds to the extremity of the latter sulcus (Plate 49, fig. 1, C). In this region is included the formation alluded to as the modified lamination of the inferior limbic arc. Vertical sections through the hemisphere behind the callosal commissure when stained by aniline black exhibit to the naked eye a remarkably defined dark belt corresponding to the granule belt just described (Plate 50, fig. 4, B). This belt can be traced outwards through the whole limbic arc and is seen to *terminate abruptly at the parietal sulcus.* On the other hand, fresh unstained vertical sections exhibit clearly to hand-magnifiers two delicate white stripes, one lying in the lower half of the first layer and the other lying within the granule belt of the second layer. These are found invariably in this region of the upper limbic arc (modified limbic type), but disappear as they bend over the marginal or sagittal angle to reach the exposed aspect of the hemisphere. They are constituted by two stripes of medullated fibres and will receive further attention when we come to describe the central projections of the olfactory organ. The depth of the individual layers of this modified upper limbic type immediately behind the corpus callosum was as follows :—

1. Peripheral cortical zone, ·325 mm. to ·372 mm.
2. Granule layer, ·372 mm.
3. Ganglionic layer, ·604 mm.
4. Spindle layer, ·604 mm. to ·744 mm.

The granule layer where deepest does not exceed ·418 mm., nor does this formation in any region attain the depth of the small pyramidal layer which it displaces and which latter usually measures ·604 to ·833 mm. deep. The substitution of this densely crowded, though shallow, layer for the deeper pyramidal series, together with the *horizontal* connexions rather than vertical, established by means of the various parallel arciform medullated belts, accounts for the notable shallowness of the whole cortex posteriorly as compared with anterior realms. Thus near the occipital pole the depth of the cortex is 1·737 mm., whilst in the neighbourhood of the frontal pole it is 2·577 mm. The granule cell is very small and averages $10\mu \times 8\mu$, having a nucleus measuring 4μ to 5μ. A large number, however, scarcely reach the dimensions of $9\mu \times 9\mu$. In form they are conical, the nucleus constituting their chief bulk, whilst the very limited and delicate protoplasm extends irregularly into several processes, the most notable being usually, although by no means universally, apical.

* Represented by dotted area on medium aspect of brain. Plate 49, fig. 1.

For a short distance internal to the primary parietal sulcus the upper stratum still contains a limited number of small pyramidal cells freely interspersed with these granule-like bodies, and giving this upper boundary a more densely packed appearance; but the lower portions of this second layer are constituted purely of granule cells. The latter resemble in every respect the intercalated belt of angular cells of the five-laminated realms of this animal, and, except in size, the smaller granules of the inner olfactory type and those distributed in the deep medullated structures of the olfactory area.

To sum up the chief features of the modified upper limbic cortex—

1. It is a four-laminated cortex with a dense belt of granules for its second layer.
2. The granule cell formation ends abruptly at the parietal sulcus.
3. The upper layer possesses a deep arciform medullated band.
4. The granule cells are disposed in serried rank by a similar arciform stripe of medulla.

The lower and anterior limbic arcs which next claim our attention comprise three distinct types of cortex—the outer olfactory, the inner olfactory, and the posterior or modified lower limbic.

Outer Olfactory Type (Plate 50, fig. 5).*

Vertical sections carried through the hemisphere, which pass through the septum lucidum, present us with four well-marked because structurally differentiated regions. These are, on the inner side or median aspect, the upper limbic arc; on the upper and outer aspect of the hemisphere the extra-limbic cortex, extending down as far as the limbic sulcus; beyond the sulcus, and occupying the basal aspect of the hemisphere, the outer olfactory portion of the lower limbic arc extends, and internal to this is a region continuous with the basal portion or head of the corpus striatum—the inner olfactory cortex.† The five-laminated cortex extending over the greater portion of the extra-limbic segment terminates abruptly at the limbic sulcus (Plate 49, fig. 1, C), immediately beneath which a wholly distinct formation commences, that of the outer olfactory cortex. This cortex is constituted by three layers, possessing but two belts of nerve-cells:—

1. A peripheral cortical zone (Plate 50, fig. 5, A).
2. A densely-compressed but shallow layer of small and very irregular pyramidal cells (Plate 50, fig. 5, B).
3. A scanty series of large pyramidal cells (Plate 50, fig. 5, C).

The outer peripheral zone has superimposed upon it, and also imbedded in its

* Area covered by this type of cortex is shown in Plate 49, fig. 1, by cross-hatching at base.

† The two lower of these regions are shown in diagram (Plate 49, fig. 8).

structure, the medullated fibres of the superficial olfactory fasciculus, which is seen in vertical sections as an oval or oblong belt, its fibres cut across transversely, and forming a notable white prominence upon the exposed surface, whilst it is also deeply imbedded so as apparently to rest in a slight sulcus of this cortical layer. The second layer of nerve-cells bends inwards in an arched form beneath it. The fibres of this superficial olfactory fasciculus (Plate 49, fig. 2, M) may be traced not only backwards towards the gyrus hippocampi, but spreading downwards into the olfactory cortex and arching outwards over its whole extent. The apex processes of the nerve-cells of the second and third layers blend with this fasciculus, whose exact connexions will be considered further on. The depth attained by this outer cortical zone varies between ·186 mm. and ·232 mm. In intimate structure it is fundamentally a supporting matrix of neuroglia, as in other regions, the nervous elements imbedded in it consisting of a dense meshwork formed by the branching of the apex processes of the nerve-cells beneath (Plate 50, fig. 5, B), and the ramifications of medullated fibres from the superficial olfactory fasciculus which are found at all depths of this layer beneath the surface. Immediately beneath the peripheral zone lies the layer of small pyramidal cells, forming but a shallow belt of densely-crowded elements, very irregular in contour, but usually pyramidal, oval, or fusiform, their apex processes bifurcating early and approaching in character very closely the small pyramidal cells of the second layer in other regions. These cells have a peculiar arrangement in clumps or appressed groups, especially in close proximity to the superficial olfactory tract. The nerve-cells vary between $18\mu \times 10\mu$ and $19\mu \times 12\mu$ in size, and possess a nucleus whose diameter is 9μ. Scattered sparsely among these smaller cells are pyramidal cells of greater dimensions, which become more frequent below the first belt of nerve-cells, forming here the third layer, through which a few really large pyramids are scattered, often measuring $31\mu \times 13\mu$, with a nucleus 13μ in diameter. The depth of the second layer is ·139 mm. to ·186 mm., that of the third or large pyramidal layer, varying from ·106 mm. (olfactory region) to ·568 mm. (gyri hippocampi). Tracing the passage of the extra-limbic formation into that of the olfactory region at the limbic sulcus, we find the layers of nerve-cells assume the laminated aspect peculiar to a sulcus. Thus the cortex becomes much shallower by the rapidly decreasing depth of the second or small pyramidal layer, and the close approach towards the latter of the ganglionic series. The second layer at the inner side of the sulcus becomes shallower and more compressed ; the larger pyramidal cells become sparse, form a less distinct layer, and are wholly absent from the innermost portion of the olfactory region, so that a clear space here intervenes betwixt the small pyramidal belt and the claustral formation beneath. Thus the second layer of the lower limbic arc is directly continuous with the small pyramidal layer of the cortex of the vault, whilst the large pyramids of its third layer are continuous with the ganglionic series of cells. The claustrum is seen beneath these layers descending from the parietal region as a deep stratum of spindle cells from ·511 mm. to 1·116 mm. in depth (Plate 50, fig. 5, D). Arching beneath the limbic

sulcus, and separated by medullated fasciculi from the corpus striatum, they appear to terminate superficially near the inner border of the superficial olfactory band. Here, as will be mentioned further on, they seem to communicate with a superficial arciform system. The axis of these cells is arranged parallel to the surface of the cortex.

Gyrus hippocampi (Plate 49, fig. 1, B). The structure of the cortex of this region is in most respects identical with that of the anterior segment of the limbic arc just described. The layers are three in number and alike in constitution, but the development of the third or large pyramidal layer is a more marked feature here. Whereas the second or small pyramidal layer was the only fully developed formation in the outer olfactory cortex, in the gyrus hippocampi the third or large pyramidal cells form a well differentiated layer, increasing in size and number towards the posterior extremity of this gyrus. Here they are identical in appearance with the pyramidal cells of the third cortical layer of human brain, showing in vertical sections six or seven branches and a long apical process. The depth of this layer also increases from before backwards.

*Inner Olfactory Type.**

Near the inner margin of the superficial olfactory fasciculus we find the commencement of a thin and peculiar cortex, which spreads over the anterior perforated space to the inner margin of the hemisphere, where, with a slight bend upon itself, it becomes continuous with the septum lucidum (Plate 49, figs. 1, 2, P). This cortex covers an area the relationship of which will be more particularly described further on, and which we shall denominate, after GRATIOLET, the olfactory area, or in contradistinction to the remaining cortex extending from it to the limbic sulcus—the inner olfactory area. The coarse or naked-eye appearances of this cortex are peculiar, as is also its histological constitution. Vertical sections carried through the hemisphere in this region will exhibit a wavy disposition of the second layer, which assumes a folded or duplicate arrangement wholly peculiar to this realm of the brain. In these V or W-shaped duplicatures the superficial layer of the cortex does not participate, so that at one time the second layer is close to the surface and at other times quite remote. The layers constituting the cortex here are three :—

1. Superficial or peripheral zone.
2. Layer of granule cells.
3. Layer of spindle cells.

1. *Peripheral zone.*—The first layer has an average depth of ·232 mm., but from the duplicatures of the subjacent layer its depth will, of course, be subject to great variation. In structure it is similar to the same layer in other regions of the cortex, differing, however, in being perforated by numerous large vessels, which pass through

* This region is seen in diagram (Plate 49, fig. 8), also by black area at base, Plate 49, fig. 1.

the cortex in straight or arched direction, within perivascular channels, which in the fresh state attain a diameter of ·110 mm. In the deeper region of this peripheral zone I find a shallow belt of arciform medullated fibres, which originating near the inner margin of the peripheral olfactory fasciculus (apparently continuous with the claustrum) is here continued inwards over the whole of the inner olfactory area.

2. *Granule cell layer.*—These cells forming the involuted layer characterising this region attain the average dimensions of 9μ long by 6μ broad, and contain a large oval or spheroidal nucleus 6μ in longest diameter. Amongst the cells of this layer we also find an abundance of very minute granules scarcely attaining a diameter of 5μ. These latter resemble the granules of the modified upper limbic cortex, but are smaller in size than these. They are common to the cortex here and to the peculiar medullated region which extends as far as the central olfactory fasciculus and anterior commissure, and may be regarded as specially the olfactory region of the nucleus caudatus. The depth of this region amounts to 3·27 mm., whilst the granule cell formation or second layer is ·116 mm. deep.

3. *Layer of spindle cells.*—Immediately beneath the wavy layer of small angular and granule cells lies a formation of fusiform cells, the elements of which attain a notable magnitude. Whilst the majority of these cells measure $32\mu \times 13\mu$, we frequently meet with far larger elements attaining the dimensions of $60\mu \times 9\mu$, with an oval nucleus 13μ in longest diameter. These spindle cells have their long axes parallel to the surface of the cortex, and lie along the course of similarly disposed medullated fibres which bend inwards to continue beneath the same layer of the septum lucidum. This cortical stratum is therefore essentially an arcuate fasciculus of medullated fibres connected with unusually large spindle cells, which bring the cortex of the inner olfactory area in connexion with that of the septum lucidum and upper limbic arc. Beneath the cortical layers above described are the densely aggregated olfactory fasciculi, which traverse the deep structure of the olfactory area, and from which vertical prolongations descend to the deeper layers of the cortex, probably fusing with the arciform medulla.*

Modified Lower Limbic Type (Plate 50, fig. 6).†

In the anterior portions of the lower limbic arc and the olfactory lobe, it was stated that the cortex was chiefly characterised by the development of the second layer as closely appressed clusters of small pyramidal cells, and with the exception of a scanty formation of large pyramids, no other nerve-cells are present. The further back we examine the lower limbic arc the greater is the development of the larger pyramidal cells, until eventually we reach a region where the large cells are much more densely grouped. Here, however, a remarkable change has occurred in the second layer, the

* Diagramatically represented in Plate 49, fig. 8, by *f*.

† Area covered by this form of cortex is the light shaded portion T to W in figs. 1 and 3.

cells of which are no longer pyramidal but swollen, inflated, globose or flask-shaped (Plate 50, fig. 6, B). They are also greatly increased in size, measuring $37\mu \times 32\mu$, or $37\mu \times 23\mu$; whilst others are more elongated, measuring $46\mu \times 27\mu$. Their nucleus has a diameter of 13μ. Their dimensions are thus *more than double* those attained by the elements of the second layer in other regions of the brain, whilst their irregular mode of branching as a bifurcate cell gives this formation the aspect of an unusually rich development of the ordinary second layer. Scattered amongst these larger cells, and descending as a distinct layer, are small pyramidal cells measuring but $23\mu \times 13\mu$, so that in this region *the series of larger cells is placed superficial to the smaller elements.* As regards either pyramidal series in other regions of the cortex, this latter feature is never observed—the upper series being invariably composed of smaller cells. Immediately beneath this third layer of pyramidal cells is a clear white belt devoid of nerve cells, and to this succeeds a belt of spindle cells (Plate 50, fig. 6, D, E). The cortex of this modified olfactory type is therefore composed of five layers :—

1. Peripheral cortical zone (depth ·418 mm.).
2. Layer of large inflated cells (depth ·279 mm.).
3. Small pyramidal cells (depth ·372 mm.).
4. Pale belt devoid of nerve cells (depth ·184 mm.).
5. Spindle series (depth ·372 mm.).

The region embraced by this formation is that portion of cortex at the extreme posterior extremity of the lower limbic arc where the upper limbic arc unites with the gyrus hippocampi (light-shaded area from T–W, Plate 49, fig. 1). It extends as far as the upper extremity of the limbic fissure seen on the median posterior aspect of the hemisphere, being bounded externally by the limbic sulcus (C) and internally by the gradually vanishing granule formation of the modified upper limbic cortex (dotted area, Plate 49, fig. 1). Sections carried *horizontally* through the occiput at this site will therefore exhibit from without inwards four types of lamination :—

1. Five-laminated type of extra-limbic cortex.
2. Modified olfactory type.
3. Modified upper limbic type.
4. Type of cornu ammonis.

Independent of the peculiar arrangement of cells and disposition of the layers in this region, a characteristic feature is acquired in the presence of two arciform stripes of medullated fibres, disposed as in the modified upper limbic cortex, one above the second layer and the other immediately beneath the same. They will be more minutely described in the section on the central projections of the olfactory lobe. For the present it will suffice to bear in mind the important fact that both these modified occipital regions of the great limbic lobe are characterised by the *double stripe of intra-cortical arciform medulla*, and by the *dense granule belt* of the one, as contrasted with the *great inflated cell formation* of the second layer in the other.

Extra-limbic mass.—Having now completed the examination of the great limbic lobe, I have next to consider the greater portion of the hemisphere which lies external to the constricting limbic arc, or that portion which in higher animals enters into the formation of a frontal, parietal, and tempo-spheroidal lobe. As in the detailed account of the various layers of the cortex in the upper four-laminated limbic arc I have anticipated many points bearing upon the structure of this extra-limbic region, it appears only necessary here to allude to the general points of divergence or similarity borne to other regions, and not to consider each individual layer minutely. The cortex, then, of this region* is five-laminated, consisting of similar layers of nerve-cells to those found in the upper limbic arc along with the interposition of a layer of small angular cells. The relative position of layers is as follows :—

1. Peripheral cortical zone.
2. Small pyramidal layer.
3. Belt of granule or angular cells.
4. Ganglionic series.
5. Spindle cells.

As regards diversity of cell formations, therefore, this is by far the richest region examined, and but a cursory glance at sections from near the occipital and frontal poles, as well as midway betwixt these points, will satisfy us that though this richly-laminated cortex has a most extensive distribution the varied layers differ much in their relative development in these different regions. Thus the small pyramidal layer is uniformly rich and deep, whilst the ganglionic series is especially developed in the anterior and median regions, and the granule and angular cells predominate in the posterior realms. Directing attention to the variations which occur in *mid-cortical regions* from within outwards, *i.e.*, from the great longitudinal fissure outwards and downwards to the lower boundary of this region, the limbic fissure, I find first, that the outer cortical zone, or first layer, *diminishes in depth*, attaining its greatest shallowness near the limbic fissure; next, the small pyramidal layer *increases in depth and richness of cells* in the same direction; thirdly, the ganglionic series tend to become distributed, after the laminar or solitary type, as we approach towards this region;† whilst in the upper realms, near the median fissure, they retain the dense confluent aspect and depth of stratum which is likewise seen in the upper limbic arc. It will likewise be observed that the intercalated layer of angular elements commencing in the posterior half of the upper limbic arc extends over the far greater area of the extra-limbic mass, and progressively increases in richness of cells and distinctness of lamination outwards and especially backwards towards the occipital pole. As already stated, this type of lamination terminates abruptly at the limbic sulcus, the small pyramidal and ganglionic series alone being continued beyond into the lower limbic arc.

* The five-laminated cortex of this region is the unshaded area at summit and sides, Plate 49, fig. 1.

† The solitary arrangement is seen well in section from sulcus of limbic lobe of Pig, *op. cit.*, plate 7.

Again, if our attention be directed to the variations observed from before backwards, *i.e.*, from frontal to occipital pole, over the extra-limbic realm, we first observe a progressive decrease in the depth of the outer cortical zone in the latter direction, with a decrease in size of the small pyramidal cells of the second layer. With this there is also associated a progressive increase of the granule or angular series which attains its greatest development posteriorly. On the other hand, the ganglionic series, from being rich in cells and deep as a stratum, at the frontal pole undergoes a progressive impoverishment along the regions midway betwixt the great longitudinal fissure and the limbic fissure, thinning out gradually to a laminar formation, whilst towards the extreme occipital cortex the ganglionic belt again becomes deep, with a layer of granules superimposed. From these particulars it may be gleaned that—

a. The cortex near the frontal pole in the extra-limbic realm approaches the type of the four-laminated upper limbic cortex.

b. The cortex midway betwixt frontal and occipital pole is a typical five-laminated formation, and represents, as does the six-laminated cortex of Man, the *common type*, because more extensively distributed.

c. The cortex of the extra-limbic realm at the occipital pole is a still further modified form of the five-laminated, but is by no means a distinct *kind* of cortex.

A notable diminution in size of the small pyramidal cells of the second layer occurs from the frontal to the occipital pole of the extra-limbic realm. Thus in front of the corpus callosum they average $22\mu \times 12\mu$, with a nucleus of 9μ, and progressively decrease in size until, on a level with the primary parietal sulcus, they measure $13\mu \times 11\mu$ (nucleus 8μ). Towards the occipital pole they again increase to $20\mu \times 11\mu$. The same features as regards size of nerve-cell were observed along the upper limbic arc ($17\mu \times 12\mu$ to $13\mu \times 9\mu$). On the other hand, the second layer in the *anterior and lower limbic arcs*, it will be remembered, increase in size towards the occipital pole, wholly lose their pyramidal contour, and from measuring $19\mu \times 12\mu$ become globose, and measure $37\mu \times 32\mu$.

It must be borne in mind that whilst the extra-limbic cortex appears to be developed out of the four-laminated cortex by the intercalation of a belt of granule cells, the modified upper limbic cortex is characterised by the granule cell-formation actually replacing the second layer of small pyramids, which is here either very defective or wholly absent.

Distribution of the Ganglionic Series.

Proceeding upon the same line of inquiry which was adopted in my former article upon the brain of the Pig and Sheep, it remains for me now to map out the area over which the ganglionic series is spread, and more especially that division of the series

characterised by a *rich confluent and deep belt of cells* co-extensive with a four-laminated cortex. Such a formation extends over the anterior half of the upper limbic arc, and stretches upwards and outwards over the exposed aspect of the hemisphere. By far the richest formation lies in the latter position—viz. : on the exposed aspect of the vault, in a lengthened strip of territory lying parallel with the great longitudinal fissure, and represented by the shaded area in the diagram.* It extends forwards well into the frontal extremity, covers the whole outer aspect of the hemisphere here, and becoming much poorer in cells, spreads along the lower confines of the extra-limbic mass, skirting the limbic fissure as far as, and even behind, the slight depression which in this animal represents the Sylvian fissure. Between these two tracts the enclosed area is spanned by a *five-laminated cortex* whose ganglionic series is poor, and distributed in the linear or solitary arrangement. The region which may therefore be considered, *par excellence*, as that of a rich ganglionic formation, is the narrow strip of cortex along the sagittal margin of the hemisphere from A to D (Plate 49, fig. 3), extending over the outer aspect of the hemisphere betwixt A and B as far down as the limbic fissure, and next to this the upper limbic arc. The far less characteristic formation adjacent to the limbic fissure, however, is interesting chiefly from the fact that it foreshadows a richer structure, which appears along this course in higher animals. It will be convenient to name these formations the sagittal and Sylvian formations of large ganglionic cells. Thus it was shown that the five-laminated cortex, with its clustered cells, in the Pig not only extends over the anterior limbic arc and frontal lobe, but bends back over the first and second parietal gyri "from their union with the ascending parietal (post-Rolandique, BROCA) towards and around the Sylvian fissure."† In the Pig, therefore, as also in the Sheep, we have demonstrated the distribution of the rich ganglionic layer over the regions bordering upon the limbic fissure. Just as in these and other allied animals we have betwixt the two regions of the clustered ganglionic cells an intermediate district characterised by a laminar arrangement of this series and an intercalated series of angular elements, so in the Rabbit a similar cortex intervenes betwixt the inner and outer series of rich ganglionic areas. We thus conclude that the fundamental type of the structure of the cortex over the extra-limbic and upper limbic realms is identical in these various animals. The dense layer of ganglionic cells bordering upon the great longitudinal fissure maintain a fair uniformity of size throughout. A large number of measurements give the following average dimensions :—

* Area shaded by small crosses, Plate 49, fig. 1.

† See fig. 3, p. 44, "On the Comparative Structure of the Cortex Cerebri." Phil. Trans., Part. I., 1880.

Plane of Section.	Length.	Width.	Nucleus.
	μ	μ	μ
Anterior to corpus callosum	32	16	13
On a plane with Sylvian depression . . .	34	16	13
Posterior to Sylvian depression	34	17	13
Posterior border of corpus callosum	34	16	12
Through superior parietal sulcus	24	18	12
Posterior to latter	31	19	13

These nerve-cells are therefore larger than those of the corresponding series in the upper limbic arc (vide table of measurements), also larger than those of the lower limbic arc, which average for the olfactory gyrus $25\mu \times 13\mu$; for the gyrus hippocampi $31\mu \times 13\mu$; and for the modified olfactory type near the occipital pole $23\mu \times 13\mu$. Larger cells occur occasionally, scattered widely apart, the largest registered attaining the dimensions of $60\mu \times 18\mu$. If these average dimensions be contrasted with those of the *second cortical layer*, in the region of the modified olfactory type (Plate 50, fig. 6, B), the important fact is disclosed that this peculiar formation consists of cells which attain a much higher average than that of the ganglionic cells. These globose inflated cells usually average $37\mu \times 32\mu$, and frequently reach the dimensions of $46\mu \times 27\mu$. These are therefore the largest nervous elements to be found throughout the cortex cerebri. The lower limb of the rich ganglionic tract extending from the frontal pole along the limbic fissure beyond the Sylvian depression, possesses cells of a smaller size than those of the corresponding upper tract. Thus in front of the corpus callosum the nerve-cells near the limbic fissure measure $27\mu \times 17\mu$, as contrasted with $32\mu \times 16\mu$ for those of the upper tract; behind the Sylvian depression those of the lower tract measure $27\mu \times 17\mu$, whilst those of the upper tract measure $34\mu \times 17\mu$.

The rich aggregation of cells in the ganglionic layer along the median exposed portion of the vault results in a deep stratum, which near the frontal extremity measures ·558 mm., and posteriorly and internal to the superior parietal sulcus ·604 mm. If this be contrasted with the pale, solitary belt in five-laminated realms, measuring but ·186 mm., its wealth of structure will be apparent. Another fact to be noted is that this layer of ganglionic cells is both deep (·604 mm.) and rich in cells in that area of the granule formation bounded externally by the primary parietal sulcus, and covers the median surface of this posterior region of the hemisphere as far back as the summit of the occipital pole. We must therefore conclude that although the ganglionic cells (next to those near the occipital pole) are the largest throughout the cortex cerebri, the distinctive feature relative to this formation is not the large size attained by the cells, as is the case in the highest of the Mammalian series—for they exhibit in the Rabbit, as in the Pig and Sheep, a remarkable uniformity throughout; but, on the other hand, this formation is especially notable for its richness in nerve-

cells—a wealth demonstrated both in depth of stratum and close aggregation of its constituents.

The Cornu Ammonis (Plate 49, fig. 7).

Peripheral cortical zone.—In the cornu ammonis this stratum may be readily seen to consist of a superficial and deeper region, which by MEYNERT and others have been regarded (in the human brain) as two distinct laminæ, representative of the first and second cortical layers elsewhere. But whereas the second layer of superficial angular cells is not developed in the Rabbit, the lower portion of this zone can scarcely be regarded as representative of a series of cells which do not appear in the most complex regions of the cortex in this animal. These two divisions have been named the nuclear and lacunar layers—the latter also termed by KUPFFER the *stratum reticulare.* On close examination of this inner or reticulated structure it becomes apparent that it clearly corresponds to the deeper portion of the peripheral zone of other cortical regions. In diverse realms of the cerebral cortex it was stated that this peripheral zone in various animals exhibited two clearly distinct portions—the outer or more superficial being often distinguished by a layer of horizontally disposed medullated fibres following the various involutions of the cortex and parallel to the surface, and extending often to a depth of one-third or even one-half that of the first layer. Now this peripheral stratum appears as the representative of the nuclear layer of the cornu ammonis. The inner or deeper portion of this zone elsewhere was seen to be composed of a dense network, formed by the apex processes of the subjacent cells dividing and subdividing in their course upwards. This was found to be the case in the Cat, Sheep, Pig, and Rabbit. In the cornu ammonis the same network is apparent, but being here entirely constituted by the apex processes of much larger cells—the ganglionic cells—it is a coarser and far more prominent formation. The whole depth of this peripheral zone is on an average ·836 mm., the outer medullated layer being about ·511 mm. The nuclear lamina, or as I prefer to term it, the medullated division of the peripheral zone, includes the following constituent elements:—

a. Band of medullated fibres derived from re-union of meshwork of the divided apical processes of ganglionic cells.

b. Numerous large blood-vessels.

c. A neuroglia matrix, containing a profusion of the ordinary nucleated connective cell; also the DEITER'S corpuscle and perivascular nuclei.

d. Spindle-form cells.

Of these constituent elements the blood-vessels are large, and dip through the medullated portion from the investing pia mater into the deeper division of the peripheral zone. Here they divide into a series of anastomosing branches, which, with the meshwork of nerve processes, gives this region its characteristic reticulated aspect.

The vessels throughout this course exhibit wide perivascular channeling, and are bordered by the usual perivascular nuclei. The connective element is similar in every respect to that found in this layer in other parts of the brain—the larger cells, measuring 9μ across, are usually nearly globular, and have a nucleus 6μ in diameter. They are very numerous, and throw off on all sides delicate fibrillar processes to constitute the neuroglia framework. The DEITER's cell is found immediately beneath the vascular investment of the cortex. Scattered through the medullated division of this cortical zone, and *especially near the confines of the reticular stratum,* are the nerve cells alluded to. They are elongate spindles, measuring $34\mu \times 12\mu$, with an oval nucleus 12μ in diameter. These cells lie parallel to the medullated fibres, throwing off branches from either pole in the direction of these fibres, but also almost invariably exhibiting a lateral process, which dips down into the cortex in the direction of the reticulated layer. These spindle cells are not numerous, and, as stated by MEYNERT, may readily be overlooked. In connexion with their presence here, it is interesting to recall similar spindle cells of great dimensions which have been pointed out as existing in certain portions of this peripheral zone in the olfactory cortex.

Striate layer.—Immediately beneath the vascular and nervous plexus constituting the reticulated portion of the peripheral zone lies the striate layer, so named after the striated aspect given by the numerous apex processes of the ganglionic layer, which radiate towards their site of common union—the nerve plexus. The depth attained by this layer averages ·558 mm., but near the commencement of the infolding of the true cornu ammonis it is much shallower, the branching of the apex processes occurring nearer to the cell. Radiating in the same direction outwards, and lying side by side with these nerve processes are numerous vessels, which rise from the ependyma of the lateral ventricles, and after supplying the medulla of the cornu, unite with the vessels of the peripheral zone (from the pia mater) through the medium of its vascular plexus. The region of these apical radiations undoubtedly corresponds to the small pyramidal layer in other realms of the cortex of the Rabbit.

Ganglionic layer.—This layer is formed by cells quite characteristic in their distribution of the cornu ammonis formation. It forms a shallow stratum varying in depth from $\cdot 093\mu$ to $\cdot 139\mu$, the average depth being $\cdot 112\mu$. The cells vary in contour, being frequently oval, elongated, or fusiform, rarely pyramidal, and much more commonly of a swollen pegtop-like contour. At the commencement of the inrolling of the cortex to form the cornu the ganglionic cells may be clearly traced into this formation, first, as a scattered series or deep belt, in which the cells approximate closer and closer until they form a belt two to five deep, in which the cells are so closely applied to each other as to be in actual contact, and form an almost unbroken file through the greater portion of the true cornu ammonis; beyond the second turn of this sigmoid fold, however, they again become more widely separated and scattered so as to form a deeper belt. In hardened sections the shrinking separates the cells widely apart, and they may be observed surrounded by a clearly defined pericellular space. In fresh sections, on the other hand,

their close approximation renders their outlines obscure except in extremely fine and carefully prepared sections. Near the commencement of the first involution where the cells are more widely scattered, these elements are observed to be encircled usually by a number of nucleated protoplasts, as are also the spindle cells, which latter have frequently such numbers heaped upon their surface as quite to conceal their real contour. These pericellular elements also tend to render the ganglionic cells of the true cornu ammonis obscure in outline. The more elongated or fusiform cell is prevalent in the lower end of the cornu ammonis or that portion bounded externally by the lower limbic arc. That portion, however, lying internal to the upper limbic arc has the characteristic pegtop-shaped cell throughout its whole extent. Each ganglionic cell besides its apex process, gives off several secondary processes from its basal extremity, and especially a primary branch from the base, which becomes an axis cylinder process. The secondary branches are directed towards the medulla and rapidly divide and subdivide within the subjacent formation (stratum moleculare). The axis cylinder process passes into the medulla of the alveus. The involuted cornu ammonis is most fully developed just posterior to the corpus callosum, and sections taken across the hemisphere at this site will therefore present us with the most extensive tracts of the ganglionic and other layers, the reticulated portion of the peripheral zone being also best studied here. The nearer we approach the inferior extremity of the cornu the more contracted is the area of section, and consequently the less extended are its nerve-cell layers, whilst the individual cells of the ganglionic series not only become more elongated in contour, but exhibit less and less of the striate formation from early subdivision of their apex processes. In the latter site, therefore, in lieu of the straight, elongated apex process of the cells becoming more and more attenuated and thus forming a forest-like structure of delicate twigs (striate layer) they commence as coarse contorted branches, which at the distance of ·046 mm. from the cell sub-divide into brush-like groups of filaments. The dimensions attained by these cells are an average length of 23μ and a width of 18μ, the nucleus measuring 13μ. At the commencement of its involution, however, where the cells are larger, more scattered, and elongated in contour, the dimensions are $37\mu \times 18\mu$ (nucleus 13μ), the apex process becoming bifurcate at from 30μ to 60μ from the cell. A few spindle cells or even pyramidal cells are found occasionally here and there at wide distances apart within the striate layer separated from the main body of cells.

Spindle-cell layer.—Beneath the ganglionic layer we come to a belt in which the neuroglia basis supports the fine fibrillar network formed by the secondary processes of the super-imposed cells. The presence of this nervous network accounts for the uniform faint staining which is here seen in aniline black preparations—a staining common to all parts of the grey cortex possessed of a network of *non-medullated* nerve fibrils and contrasted strongly with the perfectly white unstained layer of *medullated* fibres beneath this belt. Passing up from the ventricular ependyma covering the medulla of the cornu through this stratum numerous large blood-vessels are seen on their way to

the capillary plexus beyond the striate region. These vessels in hardened preparations show to a marked degree the wide perivascular channels around them. The stratum which we above described has from its fine granular aspect been termed by KUPFFER *stratum moleculare*. It is wholly absent in Man, where, according to MEYNERT, the axis processes of the ganglionic cells unite immediately with the medulla. In the Rabbit, however, the spindle cell is well represented here, not only scattered widely apart through the *stratum moleculare*, but arranged in some numbers along line of union of this stratum with the deeper medulla. Numbers of spindle cells of large size are also met with at all depths of the deep medulla of the cornu lying parallel with the direction of the medullated fibres. This spindle cell medulla communicates directly with the spindle series of the limbic lobe at the commencement of the inrolling of the cornu, and lies parallel throughout its course with the involutions of this organ. Occasionally an unusually large fusiform cell will be met with immediately beneath the ganglionic series measuring as much as $60\mu \times 11\mu$, and thus rival in size the similarly large spindle cells met with beneath the cortex of the inner olfactory region along the course of the arciform fasciculi. These fusiform elements lie embedded in and continuous with the medulla of the fornix, and usually exhibit three or more processes, one from each pole of the cell following the course of the medulla and the others lateral in origin and smaller in diameter. One of the larger processes may often be traced directly up into the layer of ganglionic cells.

Significance of the Fissures and Sulci of the Brain.

The foregoing considerations as regards the intimate structure of the cerebral cortex in the Rat and Rabbit, taken together with the results of my former examination of the cortex in the Pig, Sheep, and the Cat, lead to important conclusions relative to the significance of the fissures and sulci of the brain.

Hitherto it has been customary to regard the convolutionary arrangement as dependent in a great measure upon the progressive growth and development of the cortex, restricted and modified by the encircling cranial bones, the varied folds and complex fissures being really in this sense mere accidents of development, their uniformity of distribution in different classes of animals being due to the uniform action of the forces thus brought into play. Our investigations would lead us to a far different conclusion, nor can we, judging from our histological data, regard the divisions mapped off from each other by fissures and primary sulci as other than structurally distinct organs. In no case is this so palpable as in the various regions of the great limbic lobe, for here both a superficial survey, *i.e.*, of the structure of the cortex and an investigation of the deep medullary connexions of these regions conclusively confirm the statement now advanced. In the former memoir* I insisted strongly upon the fact that certain sulci or fissures formed sharply-defined boundary

* *Op. cit.*, p. 45.

lines betwixt regions differing in the structure of their cortex: these were the crucial and infra-parietal sulci, together with the fissure of ROLANDO. My later investigations enable me still further to extend this list by others, viz.: the limbic fissure, olfactory sulcus, and primary parietal sulcus. Thus in the Sheep and Pig we find that the crucial and sub-parietal sulci separates the five-laminated cortex, with its clustered ganglionic series, from the six-laminated cortex, with its solitary ganglion cells, the former lying in front and the latter behind these fissures. In like manner the inner extremity of the crucial sulcus formed the boundary betwixt the five-laminated cortex of the upper limbic arc anteriorly, and the peculiar granule formation of this arc behind the crucial sulcus, which extends as far as the retro-limbic annectant. In the Rat and Rabbit it is again observed that the limbic fissure, in separating the lower limbic arc from the parietal or extra-limbic mass, sharply defines two entirely distinct types of cortical lamination. Above the fissure lies the *five-laminated cortex* of the extra-limbic mass, with its intercalated series of granule cells; beneath it lies the *three-laminated cortex* of the outer olfactory region and gyrus hippocampi, whilst still further back there is found internal to it the remarkable modified olfactory cortex which has been described near the occipital pole. Within the great limbic lobe we find a sulcus, dividing two important and morphologically distinct regions. These regions are the outer and inner olfactory areas whose boundary line is the olfactory sulcus, wherein lies imbedded the superficial olfactory fasciculus. It was moreover shown that the superior parietal sulcus forms a sharp line of demarcation betwixt the five-laminated type of the parietal mass and the peculiar dense granule formation of the posterior or modified upper limbic cortex. In the higher animals, as was indicated in the former paper, the fissure of ROLANDO, here lying at the frontal pole, separates a five from a six-laminated cortex. We surely have here a most important fact, and one which, if followed up in further researches, will enable us to map out the convolutionary surface of the brain after a less arbitrary plan than the one usually adopted. The more fully I investigate the minute structure of the cortex and its deep connexions, the more forcibly am I impressed by the belief that the various fissures and sulci are not mere accidental productions, but have a deep significance of their own, dividing off the cortical superficies into *morphologically* if not *physiologically distinct organs*. Hitherto the fissures and sulci which I have found to be the boundary lines of distinct cortical realms are the following:—

1. The limbic fissure.
2. The infra-parietal sulcus.
3. The crucial sulcus.
4. The superior parietal sulcus.
5. The inter-parietal sulcus.
6. The olfactory sulcus.
7. The fissure of ROLANDO.

In the lowest of the animals examined, the Rat and Rabbit, we find the *anterior lower limbic arc* already well developed, distinct from surrounding regions, and forming the far greater bulk of the great limbic lobe. We find the limbic fissure deep and complete as far back as the region where in higher animals the retro-limbic annectant unites the limbic to the occipital lobe. Within this fissure lie the three distinct cortical regions of the outer, inner, and modified olfactory types. On the other hand the *upper* limbic arc in these animals is far from being so definitely separated from the neighbouring regions of the extra-limbic mass. The anterior or four-laminated segment of this arc is, in fact, directly continuous with the exposed cortex of the vault, no fissure, sulcus, or depression however small intervening. In connexion with this fact it is, however, important to bear in mind the identical nature of the laminated type of this portion of the limbic arc and the exposed margin of the hemisphere which bounds the longitudinal fissure (sagittal). The modified limbic type of the posterior segment of this arc, however, is sharply defined from the five-laminated cortex of the extra-limbic mass by the primary parietal sulcus. In the Pig and Sheep, on the other hand, whilst the bulk and differentiation of the lower limbic arc is maintained, there is a decided advance in this respect evident in the upper limbic arc also. The anterior portion of this arc, from its size, actually overlaps so as to appear upon the upper surface of the hemisphere, whilst a most characteristic and deep sulcus, the *crucial*, separates it sharply from the complex convoluted surface of the parietal lobe.* The oblique course of this sulcus carries it inwards to the median aspect of the hemisphere, midway betwixt frontal and occipital pole, where it meets the subparietal sulcus, regarded by BROCA as the continuation upwards of the limbic fissure. This latter sulcus, sweeping backwards, does not join the limbic fissure posteriorly, being separated by the retro-limbic annectant, but as the latter annectant corresponds to the region which in the Rat and Rabbit is characterised by the modified olfactory type of cortex, this sub-parietal sulcus forms a line of demarcation betwixt the latter type of cortex and the granule formation of the upper arc. The mapping out of distinct morphological areas exhibited in the lower limbic arc of the smooth brain of the Rat and Rabbit, is a feature which in the convoluted brain of the Pig and Sheep becomes extended to the upper limbic arc also through the medium of the crucial and subparietal sulci. Moreover in these convoluted brains the deep inter-parietal sulcus also divides two highly characteristic formations. Still higher, as in the Carnivora, the fissure of ROLANDO constitutes a similar limitary zone, the cortex of the ascending parietal (post-Rolandique of BROCA) being six-laminated; that of the ascending frontal five-laminated.

* *Op. cit.*

Section 2.—Central Projections of the Olfactory Organ.

The Olfactory Lobe and Bulb.

The olfactory lobe is constituted by a tubular prolongation of the cerebral cortex given off from the inferior aspect of the anterior pole of the hemisphere. Within the confines of the limbic fissure its cortex is directly continuous with that of both extremities of the limbic lobe along the lower and lateral aspects of the brain, whilst above and outside the boundaries of the limbic fissure it is overlapped by the projecting frontal extremity of the hemisphere, with the cortex of which its surface is also continuous. Its continuity with the anterior extremity of the upper and lower limbic arcs thus completes the circuit made by the great limbic lobe.

The summit of the olfactory lobe is capped by the olfactory bulb, which completely ensheaths its extremity and receives the olfactory nerve fibres.

The connexions of the olfactory cortex, inclusive of the bulb, are in this animal both complicated and extensive—complicated in that its medulla brings it into relation with most diverse regions of the brain, and extensive in so far that its fibres are projected back into the occipital pole of the hemisphere, and embrace in their circuit the whole extent of the limbic arc, thus associating the most distant realms of the brain in direct organic connexion. For convenience of description as well as upon anatomical grounds, we may consider the olfactory medulla as consisting of the following distinct systems :—

1. A central decussating and commissural fasciculus.
2. A connecting system with the striate body.
3. An arciform series.
4. A superficial medullated band.

1. *Central fasciculus.*—A rapid convergence of fibres from the bulbus olfactorius constitutes the origin of a central medullated core for the olfactory lobe, which soon becoming almost cylindrical in contour courses backwards through this lobe, and arching slightly outwards plunges into the anterior extremity of the caudate nucleus. Owing to its outward curve, vertical sections through the frontal extremity exhibit an oval contour of this fasciculus, such oblique sections measuring 1·3 mm. in its greater diameter, by ·78 mm. in its shorter diameter. It is, however, a uniformly cylindrical fasciculus, its usual diameter being ·87 mm. Receiving no fresh addition of fibres, the central olfactory fasciculi of both hemispheres attain their greatest distance apart within the corpus striatum (4·76 to 5·046 mm.), and thence converge towards the descending pillar of the fornix, passing in this course slightly upwards in relation to the cortex at the base, and lying betwixt the corpus striatum on the outer side and the thickened folia of the septum lucidum internally, in close relationship to the floor of the lateral ventricles. In the Rabbit, the central canal is seen lined with endothelium,

and surrounded by the central medullary fasciculus, forming a direct communication between the olfactory lobe and the lateral ventricle. Still converging, these two fasciculi decussate in the median line immediately in front of the pillars of the fornix, constituting by this convergence the anterior commissure of the cerebrum, being in this latter course imbedded in the septum lucidum. The resultant fibres of this decussation pass out from the commissure as a compact fasciculus, and are not projected directly backwards, but arch *suddenly outwards*, passing through the substance of the corpus striatum. In this course the fasciculi of either side diverge so rapidly that they lie very nearly in one and the same line, a single vertical section through the hemispheres presenting us with the commissural band and both posterior fasciculi as far as the outer border of the striate body. To follow the further course of these posterior projections from the olfactory bulb, horizontal sections of the cerebrum of the Rat should be examined, and it will then be found that each fasciculus passes through the striate body, and upon reaching its most external border each olfactory band sub-divides into several secondary fasciculi similar in appearance to those which result from the union of the fibres of the first link of the projection system at their connexion with the receiving surface of the corpus striatum (Plate 49, fig. 9, A).

These sub-divisions of the posterior olfactory fasciculus curve directly back into the occipital pole (Plate 49, fig. 9, B). If *vertical* sections of the hemisphere at this site be examined, the connexions of the cortex with the corpus striatum by the projection system of fibres will be found to be chiefly affected by the upper surface of the ganglion, with which a large bulk of coarse fasciculi are connected (Plate 49, fig. 10, A); yet the *whole outer aspect* of the ganglion in like manner receives numerous fasciculi, which form a complete medullated investment over its outer surface. This medullated investment being augmented by fewer fibres, and yet fewer at lower levels, eventually thins off into an insignificant tract (Plate 49, fig. 10, B). Now it is by no means improbable that a certain number of minute fasciculi in the Rat pass from the sub-divisions of the posterior olfactory fasciculus upwards along this medullated tract. I have repeatedly imagined that I could trace such a connexion, and if this turns out to be correct then we have here a distribution similar to although far more restricted than what I have assured myself is the case with the Rabbit's brain. The position of this posterior olfactory fasciculus from the anterior commissure in its course through the corpus striatum is parallel to the base of the lenticular wedge, lying in fact betwixt its two main divisions, as may be clearly seen in horizontal sections taken at the proper plane, in which will also be very evident the fact, that whilst these fibres run directly backwards, the majority of the projection fibres of the corpus striatum pass directly outwards or forwards to the cortex (Plate 49, fig. 9, A–C). The olfactory fasciculus, prior to the formation of the anterior commissure, measures in its shortest diameter ·78 mm. to ·87 mm.; the fasciculus emerging from the commissure, as it leaves the septum lucidum to enter the corpus striatum, measures but ·52 mm. This reduction in bulk is due to the absence of a series of fibres which run from one olfactory bulb to

that of the opposite side, as a purely commissural system. This of course is in accordance with the fact indicated by GRATIOLET, MEYNERT, and others, that in the Rodentia and Carnivora, where the olfactory apparatus is largely developed, the great bulk of fibres proceeding from the anterior commissure communicate with the olfactory lobe; whilst in Man and Apes, where its development is small, the larger portion of the commissure is distributed backwards to the occipital and to the temporo-sphenoidal lobes. The central olfactory fasciculus behind the anterior commissure exhibits a notable difference in its distribution in the Rabbit and the Rat, a divergence which has an important bearing upon the functional relationships of the olfactory lobes. In the Rat, as has just been stated, the fasciculus passes outwards through the corpus striatum, and *immediately* upon reaching its outer border divides into a brush-like head of nerve bundles, some of which probably unite with the projection fasciculi passing through them up to the vault, but by far the most extensive portion turns back, and runs towards the occipital pole of the hemisphere (Plate 49, fig. 9). In the Rabbit, on the other hand, when the posterior olfactory fasciculus reaches the outer surface of the corpus striatum it does not, as in the Rat, break up into numerous diverging bundles, but bends upwards and ascends as a more or less compact fasciculus in contact with the outer surface of the ganglion (Plate 49, fig. 11, A). Upon reaching the level of the upper pole of the striate ganglion it meets with the accumulating mass of the projection and callosal systems (C, D), and at this spot it suddenly breaks up into an extensive brush-like head of fibres (B), which pierce through the mass of the projection system, and are thence directed towards the cortex of the inner margin of the hemisphere, *i.e.*, the margin bounding the great longitudinal fissure (E). In vertical sections which have been carried successfully through the plane of the posterior commissural fasciculus, we may readily trace it—first in its horizontal course through the striate ganglion, next curving round and up the outer aspect of that ganglion, and lastly on its arrival at the upper pole, grasping, as it were, by a mass of tentacular-like extensions, the base of the projection system, decussating freely with the callosal fibres, meeting them from an opposite direction, and with the projection fibres betwixt striate body and cortex, which in part traverse the same course.* What is the destination of this important system of fibres? It appears indeed to form that extensive arcuate system which lies beneath the cortex of the summit of the hemisphere at these planes. This arcuate system may be readily seen lying betwixt the cortex of the vault and the great mass of the projection and callosal systems above the corpus striatum (Plate 49, fig. 11, F). They therefore are directed nearly at right angles to the radiating callosal fibres for the cortex of the vertex, and running parallel to the surface of the cortex, terminate in the region of the large ganglionic cells which have been referred to as seen in the cortex along the inner margin of the vault. In short, then, the olfactory bulbs of the Rabbit are thus brought into direct and decussating connexion through an extensive course with the specialised cortex of the inner

* The whole of this course is represented in Plate 49, fig. 11.

marginal aspect of the brain in its anterior regions—a region proved by FERRIER to have motor endowments. In the Rat, on the other hand, this fasciculus is brought into relationship not so much with the motor cortex as with the cortex of the occipital pole, with which it has most extensive connexions. No doubt need be entertained upon these facts after a careful examination of horizontal and vertical sections of the frozen brain of these animals, and by dissection and teasing out of these structures. In vertical sections I have repeatedly succeeded in tracing the posterior commissural fasciculus upwards towards the projection system above, and have teased out, by means of a dissecting needle, the whole of its course from the anterior commissure to the brush-like head, leaving it a compact band of fibres entirely separated from the surrounding structures.

The olfactory lyre.—This is a structure which I have ventured to name by what appears a very appropriate term when its configuration is thoroughly understood—it has up to the present been entirely overlooked in descriptions of the olfactory apparatus. MEYNERT distinctly states, when describing the posterior extensions from the anterior commissure in his classical work on the brain of Mammals,* that the fasciculus passes "uninterruptedly through the corpus striatum." This statement is, however, undoubtedly an error, and it requires but a careful examination of vertical sections through this commissural tract in the Rabbit or a dissection of the fresh brain of the Rat or Rabbit to show not only that such is not the case, but that MEYNERT and others must have entirely overlooked here a structure which is most peculiar and important in its bearings. Vertical sections through the fresh brain of the Rabbit show very distinctly oval fasciculi of no mean size separating the strands of the posterior olfactory band, largest and most numerous near the anterior commissure (Plate 49, fig. 11, G). They consist of divided medullated fibres, which distinctly traverse the structure of the olfactory fasciculus from the portion of the striate body lying in front to that lying behind the commissure. In passing through the olfactory fasciculus a very apparent increase in the size of this tract is occasioned by this separation of its strands, so that a great oval enlargement characterises the earlier portion of this fasciculus in the Rabbit. A dissection of the brain of the Rat will indicate still more readily the nature of the structures here exhibited. Such a dissection will be described in detail further on—let it suffice here to state that by this method we expose a series of delicate fasciculi of medullated fibres passing from the posterior olfactory band forwards parallel to the central olfactory fasciculus. In part, these fibres traverse the structure of the olfactory band at right angles to its course, passing thus into the corpus striatum behind it, whilst others attached to the anterior margin of the same band curve inwards to accompany the rest of its fibres across the commissure. In passing forwards these fibres form a delicate floor or dissepiment betwixt the structure of the corpus striatum proper and that portion of the same ganglion which forms the olfactory area. This delicate sheet of medullated strands occupies a triangular space bounded internally by

* STRICKER'S 'Handbook,' Sydenham Soc. Trans.

the central olfactory fasciculus, behind by the posterior olfactory fasciculus, and externally and deeply by the superficial olfactory medulla, and betwixt these boundaries the fibres pass forwards like the strands of a lyre in relation to its several sides—hence the term by which I have denominated this structure.

Tænia semicircularis.—This long arciform band of medullated fibres arising from the summit of the gyrus hippocampi follows the curved inner surface of the caudate nucleus through the whole of its course, and consists of superficial and deeper-seated fibres, the latter connected with the ganglionic structure of the caudate nucleus. It has been affirmed by numerous authorities that this arciform band terminates in the descending pillar of the fornix.* That the more superficial fibres so terminate I will not deny; but I have hitherto failed in *these animals* to assure myself of the fact. Of its deeper fibres I can speak with confidence. They not only *do not terminate* in the fornix, but end in two distinct directions, the deepest curving downwards to enter the anterior perforated space (Plate 49, fig. 12, 2); the fibres above this series arch inwards and forwards to enter the posterior commissure (Plate 49, fig. 12, 1). The latter connexion is a most important one to recognise, and of its existence I have repeatedly assured myself by horizontal and vertical sections. The fibres enter the commissure from behind in such a direction as to ensure their decussation within it. The cortex of the gyrus hippocampi and caudate nucleus are thus brought into crossed relationship with the olfactory bulbs.

2. *Connexions with striate ganglion.*—The anterior extremity or head of the caudate nucleus bends downwards to the base, and approaching the median line is separated from the ganglion of the opposite side by the mass of the septum lucidum. At the base the ganglion becomes almost superficial, being merely covered by a very thin layer of cortex, which is continuous with the general surface of the olfactory lobe. Medullated fibres from the cortex of the olfactory lobe and the granule layers of the bulb pass from before backwards into this basal extension of the caudate nucleus in numerous bundles, which in vertical sections appear mapped out into triangular wedge-shaped spaces by the large vessels traversing this region (pars perforata antica). This basal region of the corpus striatum, the olfactory field of GRATIOLET, is best studied in fresh preparations by horizontal sections carried across the hemispheres. The brain is placed on the section plate of a microtome with its base downwards, frozen to the height of a few millimetres, the unfrozen portion removed, and then successive sections should be made down as far as the cortex of the base. All these sections examined fresh will prove most instructive. A section carried in this way through the cortex shows this basal or olfactory realm of the brain to be clearly mapped out into two very distinct areas. One, the most internal, is of pyriform contour, its narrow end continuous with the olfactory lobe, its larger end directed backwards. This area constitutes the base of the corpus striatum and has a peculiarly characteristic structure. The other, or outermost area, is constituted by a continuation of the olfactory cortex with the lower

* MECKEL, ARNOLD, JUNG, and LUYS.

limbic arc, and is sharply separated from the former area by the superficial olfactory fasciculus, whilst on its outer side it is of course bounded by the limbic sulcus. Following exactly the outer border of the pyriform area, the superficial olfactory band is naturally at first curved outwards, and then inwards towards the Sylvian depression. In sections taken across a slightly higher level the same regions are distinctly seen and their structure rendered clear. The innermost area is now seen to consist of numerous oblong and elliptic masses of grey matter enclosing nerve corpuscles; these grey nuclei vary much in size, but usually measure ·348 mm. to ·870 mm. in length by ·204 mm. to 300 mm. in width. They are closely embraced by bundles of medullated fibres, which form dense fasciculi betwixt them and are all directed from before backwards. They originate in the cortex of the olfactory lobe and pass through this ganglionic region. Mingled with these is a separate system of fibres which arise from the granule layers of the olfactory bulb, and coursing chiefly along the inner basal aspect of the olfactory lobe also enter this olfactory area, but do not form fasciculi. Their peculiarity consists in their running as separate fibres very irregularly, as bending, decussating and crossing each other in various directions so as to give the impression of their forming an open meshwork. These nerve fibres measure ·002 mm. to ·004 mm. in diameter. They penetrate the oval nuclei, and are found throughout their substance. As they do not extend beyond this region they terminate almost certainly in the nerve-cells of its grey masses. The outer surface of this olfactory region is covered, as was indicated by MEYNERT, by a thin layer of cortex, whose structure has already been fully described (p. 714). In passing through the olfactory area this deep mass of medulla is disposed in numerous longitudinal divisions or clumps well shown in vertical sections, from which smaller fasciculi are seen to descend to the cortex of the base, where they become apparently continuous with the arciform medulla superficial to and beneath the second cortical layer. Continuous with this deep olfactory medulla is a minor segment given off from the superficial olfactory fasciculus along its inner margin, and which can be best demonstrated by longitudinal sections through the hemisphere. The following scheme represents in a diagram the numerous systems of medullated fibres seen in vertical sections through this olfactory area (Plate 49, fig. 8). In the first place, we trace the cortex from the limbic fissure (*a*) downwards beneath the superficial olfactory fasciculus (*b*) prolonged over the basal aspect of the caudate nucleus. Its second layer is seen disposed in the peculiar duplicatures described, and beneath which lie the clumps of deep olfactory medulla seen in cross section (*m*) forming massive fasciculi contrasted strangely with the more distant fasciculi of the corpus striatum proper. Betwixt the deep medulla and the second layer is the deep arciform belt (*d*) with its great spindle cells apparently continuous with the claustral formation externally (*c*) and with the arciform medulla passing up the septum lucidum internally (*e*). Descending from the deep medulla into this arciform belt are numerous vertical fasciculi (*f*), which may also probably form connexions with the second layer of the cortex. The deep medulla gives off laterally a dense mass of fibres which ascend

deeply within the substance of the septum lucidum (g), whilst the cortex of the septum is seen to possess a double arciform belt, one superficial to its second layer (h), and the other beneath these cells (k). These arciform stripes communicate by vertical intermediate fibres with each other in their course upwards to the corpus callosum.

From this olfactory area an important medullated fasciculus descends to enter the motor columns of the cord, hence affording a direct channel for the impulses propagated on excitation of the olfactory bulb. The double connexion with motor columns of the medulla and the cerebral cortex is the usual condition in Mammalia, although, as BROCA has indicated, the connexion with the *cortex* alone is the only constant feature.

3. *Arciform fasciculi.*—If the olfactory lobe be reflected downwards, away from the frontal pole, an upper medullated connexion betwixt the former and the hemisphere, may be traced lying invariably over the central canal of this lobe. But by far the more important arciform fasciculi form two series, which taking origin in the cortex of the olfactory lobe, are destined for the gyrus fornicatus and posterior regions of the brain. In vertical sections through the frontal end of the hemisphere, near the commencement of the caudate nucleus, the central olfactory fasciculus is seen in transverse section, imbedded in the head of this nucleus, which rises dome-like above it. Descending from the region of the central medulla of the hemisphere, are two medullary finger-like processes which appear to grasp the caudate nucleus betwixt them. The outer is constituted by fasciculi arising from the external borders of the caudate nucleus and disappears in the central medulla. The inner lies parallel with the central mass of medulla, but is wholly distinct from it, and constitutes the arciform fasciculi, which originate in the cortex of the olfactory lobe at the base and median aspect, and curving up the inner side of the hemisphere is closely connected with the cortex of the upper limbic arc. At the median aspect, where the upper limbic arc unites with the olfactory cortex, numerous medullated fasciculi arising from the latter follow the bend of the hemisphere, and thence arching strongly inwards come into relationship with the under surface of the corpus callosum, and turning backwards, course along its inferior aspect, whilst other fasciculi pierce its structure and join the arciform system of the gyrus fornicatus, which rests upon the upper surface of the corpus callosum. (Plate 49, fig. 12, ^{7}). At its origin this important fasciculus is seen in vertical sections, ascending in a sigmoid curve, with the convexity first inwards and then outwards towards the under surface of the callosal commissure. A little further back the septum lucidum is found to the inner side of the olfactory area. In this animal it appears as a largely-developed structure, heart-shaped in vertical section, and formed of two lateral folioles uniting centrally, and not enclosing a ventricle betwixt them as in Man. Through the substance of the septum a large number of medullated fibres ascend to the inferior aspect of the corpus callosum (Plate 49, fig. 8, G). The longitudinal band formed by the arciform fibres of the olfactory and upper limbic

cortex is distributed eventually to a peculiar region already described, near the occipital pole of the hemisphere, which is covered by cortex of the modified upper limbic type. This termination will be described when I refer to the central expansions of the olfactory medulla.

4. *Superficial olfactory fasciculus* ("External root").—This fasciculus appears, from a surface view, as a flattened white lamina covering the basal aspect of the olfactory lobe. Widest in front, it encircles the greater surface of this lobe, grasping its lower, outer, and portion of its upper aspect. Thence directed backwards, it sweeps round the olfactory area, forming, as already stated, its outer boundary, and becoming rapidly attenuated, runs as a delicate white streak inwards, in a direction which, if continued, would pass nearly at right angles across the origin of the optic tracts. In this, its latter course, it passes over that slight furrow which here indicates the Sylvian fissure, and is lost in the substance of the gyrus hippocampi. Vertical sections show that this fasciculus is not a mere flattened lamina, but a thickened oval or oblong band, which is sunk to a little depth in the peripheral zone of the cortex, covered externally by a delicate layer of DEITER's cells connected with its pia mater, from which large vessels dip vertically through its substance and enter the subjacent cortex.

In what manner does this medullated band terminate? It has long been known that in Man and the higher Mammals the external olfactory medulla ends in the temporal and occipital lobes, but in these animals it is seen by the naked eye that a rapid attenuation is undergone ere it reaches the Sylvian furrow (Plate 49, figs. 1, 2, M). To comprehend its distribution we must examine closely vertical and horizontal sections through this region anterior to the Sylvian depression. In vertical sections the superficial olfactory fasciculus forms the inner border of what we have termed the external olfactory region, limited outwards by the limbic sulcus. The cortex of this region is composed, as already stated, of the three layers—the peripheral zone; the irregular and angular cells; the large pyramidal layer. Now beneath the lowest layer of this cortex, at variable depths, is found an important formation of spindle-cells, which taking the reclinate position as regards the surface, descends from the extra-limbic portion of the hemisphere. This belt of spindle-cells is the representative of the claustral formation of higher Mammals, and is directed towards the surface of the cortex below, along the inner margin of the superficial olfactory fasciculus. It forms therefore a deep belt, dividing off the olfactory area from the external olfactory regions (Plate 49, fig. 8, *c*). Having noted this fact, a horizontal section should be taken through the hemisphere, close to its basal cortex, as was done for the examination of the connexion of the olfactory lobe with the olfactory area. If such a section pass through the deeper part of the superficial olfactory band we shall note that whilst its outer fibres are long and continued uninterruptedly backwards, the innermost fasciculi constantly tend to bend outwards and pass through and across the longitudinal band, arching in fan-like manner over the whole external olfactory region as far as the limbic

sulcus. This passage of the inner marginal fibres of the band into the cortical substrata must eventually lead to its total disappearance. These fan-like radiations are continuous with the cells of the cortical layers; yet it does appear as though a connexion was also established betwixt its innermost fibres and the claustrum, which latter formation, however, is mainly continuous with the arciform spindle-celled medulla of the olfactory area (Plate 49, fig. 8, *d*). Prior to the arrival of this superficial medullated band at the Sylvian furrow a notable diminution in its width has occurred, apparent to the naked eye. This is due to the detachment from its margin of a large proportion of fibres which have already been alluded to as running continuous with the deep olfactory medulla within the olfactory area. It has been usual to speak of the central projections of the olfactory medulla under the terms olfactory roots, an *external, middle, and internal root* being usually those described in higher animals. A fourth also is described as a *superior root,* connecting the upper surface of the olfactory lobe to the hemisphere. By the external root is indicated what I have above described as the superficial olfactory fasciculus; the connecting system with the striate body is identical with the so-called middle root, whilst the arciform series includes the remaining two roots, the internal and superior.

Dissection of Basal Olfactory Regions.

The tracing of the coarser strands of medullated fibres by microscopic examination of sections, should invariably be supplemented, where possible, by frequent dissections which often enable us to fully confirm by this second method results arrived at by the former. As regards the olfactory regions at the base the following points may by this method be satisfactorily demonstrated in the Rabbit and the Rat:—

a. Uninterrupted course of the central olfactory fasciculus into anterior commissure.
b. Projection of posterior olfactory fasciculus into the occipital lobe.
c. Connexion of the latter fasciculus also with the cortex of the vertex.
d. Peculiar connexion of the same fasciculus with the corpus striatum.
e. Relationships of olfactory area at greatest depth below cortex.
f. Descent of the tænia semicircularis into olfactory area.

The above facts may be confirmed by placing the brain of the Rat in its natural position with the vertex upwards, and keeping it during dissection moistened occasionally by a few drops of a 2 per cent. solution of common salt. With a delicate pair of dissecting scissors the membranes stretching across between the hemispheres are divided through their whole length, and the latter sliced off horizontally outwards upon a level with the corpus callosum by a sharp and fine scalpel. This commissure is next divided along the median line from behind forwards, each segment being turned outwards. Such a section exposes the corpus striatum in its extra- and intra-

ventricular portions placed in front of the cornu ammonis. In the median line separating the two striate bodies lie the double leaflets of the septum pellucidum. The callosal fibres are seen to meet those ascending from the internal capsule and upper pole of the ganglia. If the extra-ventricular nucleus be pressed gently outwards away from the caudate nucleus, we observe numerous white fasciculi beneath its surface arching upwards parallel to the latter to enter the projection mass at the upper pole, whilst running parallel with the converging tract of the fornix, and closely connected with the whole inner border of the caudate nucleus, is the fairly broad white band—the tænia semicircularis. By means of a fine dissecting needle and camel-hair brush the whole remaining dissection may be completed. First, the septum pellucidum is gently raised from behind and thrown forwards, the hemispheres pressed asunder so as to expose the descending pillar of the fornix, in front of which the anterior commissure crosses from one to the other hemisphere. By means of the needle the continuation of this commissure, with the olfactory lobe of one side, may be most readily traced, and upon cautiously teazing out the substance of the striate body on one side, the continuation from the commissure outwards through its substance may be quite as easily traced. We now see gleaming deeply through the basal structures of this region a pale band which may be regarded as the outer side of a remarkable triangle, the inner side being constituted by the central olfactory fasciculus, and the base by the anterior commissure and its posterior extension. Now this triangular area is the deeper portion of the pyriform region recognised at the base as GRATIOLET's olfactory area. Closely examined by a hand magnifier we now see the very peculiar structure alluded to as the "olfactory lyre." Gently raise by the needle the posterior olfactory fasciculus and examine also with a lens. From its anterior border arise numerous delicate fibres constituting more or less fine fasciculi, the largest arising near the anterior commissure, whilst a few delicate offsets are given off from the commissure itself. Whilst these fasciculi curve inwards and appear *continuous with the olfactory tract into and through the commissure,* other fasciculi may be seen passing through the structure of the posterior olfactory band directly backwards, separating its strands and *emerging behind to enter this region of the corpus striatum.* Traced forwards these delicate fasciculi lie parallel to and on a plane with the central olfactory fasciculus, forming as it were a floor for this triangular space (the strands of the lyre), and in fact sharply defining the upper limits of the olfactory area from the structure of the caudate nucleus proper. With the scissors divide these fibres along their line of connexion to the posterior olfactory tract, and teaze out with the needle the structures lying immediately beneath. We now see by means of a low power, and even by the naked eye, the coarse fasciculi enclosing betwixt their strands the oval grey nuclei of the olfactory area. Next, by a delicate dissection with needle and moistened brush, the posterior olfactory fasciculus may be followed from the outer margin of the striate nucleus backwards; its brush-like division here sending a small detachment of fibres upwards along the outer aspect of the corpus striatum to reach the vertex. The

posterior division of the brush may readily be traced into the inferior arc of the great limbic lobe, its fasciculi never rising above the level of the limbic sulcus. They are ultimately distributed to that peculiar region at the occiput characterised by the modified olfactory cortex.

It now remains for us to follow up the extensions of medullated fasciculi from the olfactory lobe, and to trace the expansions into the distant cortical areas of the central olfactory and arcuate olfactory systems. Prior to doing so, it will be advisable to consider the structure and cortical connexions of the corpus striatum and callosal commissure.

Corpus Striatum and its Cortical Connexions.

Corpus striatum.—This ganglionic body exhibits in these animals, as in higher members of the animal kingdom, a marked division into lenticular and caudate segments, or, in other words, extra- and intra-ventricular nuclei, which assume also a higher level as compared with the thalamus, since the largely developed cornu ammonis and the bulky fibrous fornix commences at higher and anterior planes, and not, as in Man, *behind* the thalamus. These structures therefore intervene betwixt the cortex of the vertex and thalamus, and displace the latter to a lower level, so that sections carried horizontally through the upper part of the hemisphere will exhibit the striate body and cornu ammonis cut through in one and the same plane. Anteriorly the corpus striatum exhibits a large rounded head, which bends downwards to the base of the hemisphere within the confines of the superficial olfactory fasciculus. Posteriorly it becomes rapidly attenuated and is continued as a small cylindrical belt of grey matter—the tail of the caudate nucleus, which curves backwards and downwards within the descending horn of the lateral ventricle to terminate in the inferior limbic arc, near the summit of the gyrus hippocampi (Plate 49, fig. 10, C). To study the form and relationship of the striate body, vertical sections should be examined passing through the septum pellucidum in front of the optic commissure. This ganglion is then seen as a large irregularly pyriform structure, its greater mass directed upwards, its upper and outer border nearly concentric with the surface of the hemisphere (Plate 49, fig. 12, 4),* whilst the inner or intra-ventricular border lies partly adjacent to the thick foliole of the septum lucidum (fig. 8, *b*), and at the angle of union with the latter the transverse section of a compact band of medullated fibres is seen, the central olfactory fasciculus (Plate 49, fig. 8, *h.*). The true structure of the corpus striatum ends upon a level with this olfactory fasciculus, and is mapped out by a succession of fasciculi, which are cut across and lie in a continuous line from the central olfactory fasciculus to the outer margin of the ganglion. These fasciculi are of greater size than those beneath them, and are constituted by the strands of the "lyre" already alluded to. Beneath this line the striate nucleus still extends as far

* The diagram (fig. 8) exhibits in outline a part of the caudate nucleus and its full basal relationships.

as the base, forming the modified structure referred to as the olfactory area, and which is here covered by a thin layer of cortex.* The outer margin of the striate body is sharply differentiated from the outer olfactory realm (lower limbic arc), and terminates abruptly at the inner margin of the superficial olfactory band, to which point run the fibres of the claustral formation (Plate 49, fig. 8, *c*). On the inner side, at its base, we find this olfactory area of the corpus striatum bounded not only by the central olfactory fasciculus, but by sheaves of fibres arising from the cortex of the olfactory lobe (Plate 49, fig. 8, G, *g*), and running as the arciform fibres up the septum lucidum to reach the under surface of the corpus callosum. In these anterior realms the internal capsule which separates the two main divisions of the striate body is not as yet clearly differentiated, and hence the large oval mass is constituted by the blending together of the caudate and lenticular nuclei, and the fasciculi here being chiefly projections from the cortex of the frontal lobe are seen in transverse or oblique section. To obtain a good view of the fibres radiating from the frontal pole through the structure of the corpus striatum vertical sections must be taken across the hemispheres. At the summit or upper pole of the striate body (Plate 49, fig. 11, H) the fibres of the corpus callosum (D) meet those of the projection system from the cortex to the basal ganglia, and at their line of intersection mark off the intra-ventricular (K) from the extra-ventricular portion (L). We have therefore in such sections a large ganglionic mass formed by the blending of the two striate nuclei, enclosed in a concentric manner by the hemisphere, and exhibiting the following systems of fibres: the callosal fasciculi (D); the striate radiations to cortex (C); the claustral formation (Plate 49, fig. 8, *c*); the external (*b*); median or deep (*m*); internal and central olfactory fasciculi (G and *h*). In vertical sections carried through the hemisphere of the Rabbit on a plane with the anterior commissure the distinction betwixt the two nuclei of the corpus striatum is very obvious. Here the caudate nucleus lies reclinate upon the sloping oblique side of the internal capsule, measuring from 9 mm. to 10 mm. in its longer, and 2·5 mm. in its shorter diameter, its upper pole directed upwards and outwards, receiving the radiating fibres from the cortex; its inferior pole directed downwards and inwards as a thin prolonged margin, exhibiting on its ventricular aspect the transverse section of the stria cornea (Plate 49, fig. 12, 4). Beneath the stria cornea with the structure of this inferior pole are nerve fasciculi, which in part pass downwards into the anterior perforated space (Plate 49, fig. 12, 2) (olfactory area), whilst a few arch inwards and are directly continuous with the anterior commissure (Plate 49, fig. 12, 1). Beneath the sloping roof formed by the internal capsule lies the lenticular nucleus, which is distinctly wedge-shaped in form, its base directed outwards and curved concentrically to the surface of the hemisphere, its apex directed downwards and inwards terminates in the internal capsule (Plate 49, fig. 9, D). The lenticular nucleus appears to consist of outer and inner segment; the inner,

* Vide Plate 49, fig. 8. All structures below *h*.

forming the peduncular portion and apex of the wedge (Plate 49, fig. 9, D), contains a far greater proportion of fibres than the outer, which are consequently much more closely approximated, consisting, as MEYNERT indicates, of fibres extending from the outer segment, as well as fibres originating afresh in itself. The further our examination of these nuclei by vertical sections extends, the more restricted becomes the dimensions of the lenticular nucleus, the mass of the thalamus intervening until on a plane with the origin of the pineal peduncles; its extent is very insignificant,* whilst the tail of the caudate nucleus (Plate 49, fig. 10, D) and the stria cornea are seen as two small oval bodies, separated from it by the intervening cortical connexions of the ganglia. In these posterior planes, vertical sections passing through the tuber cinereum will exhibit within the substance of the inferior limbic arc two noteworthy structures: first, a compact cylindrical band, consisting of some thirty or more fasciculi of medullated fibres, which results from the convergence of fibres from the cortex of this region, and is really the temporal extension of the stria cornea; and secondly, just external to it lies a somewhat oval nuclear grey body, the tail-like prolongation of the caudate nucleus (Plate 49, fig. 10, C). In sections through the hemispheres at that site where the retiring optic tracts are concealed betwixt the crus cerebri and hemisphere, the stria cornea will appear to a certain extent of their course cut lengthwise and entering the substance of the limbic lobe external to the optic tract (Plate 49, fig. 10, E).

Coronal projections to the motor ganglia and internal capsule.—Traced from the cortex downwards it is found that the whole marginal aspect of the hemisphere at the vertex and for a certain distance outside the median line, constitutes the area whence the coronal radiations arise which converge to the internal capsule and corpus striatum below. Upon arriving at the centric pole of the corpus striatum, the fibres form a dense projection mass, which in the form of small fasciculi spread out and almost completely enfold the upper and outer aspect of this ganglion, the innermost series entering the ganglion direct, the outer fasciculi proceeding along the arched surface of the lenticular nucleus to enter it at its outer aspect, whilst the intermediate fibres terminate at various points along the intervening surface (Plate 49, fig. 10, A). The receiving surface or centric pole of the striate body is therefore a very extensive one, being constituted by the whole of its upper and greater part of its outer aspect. The above description of its cortical connexions holds good only as regards that region where the centric pole of these ganglia attains its greatest height, viz.: anterior to the thalamus where the corpora striata lie in closer contiguity. To study its exact distribution a series of vertical sections of the brain of the Rat should be examined at different planes from before backwards. Thus, in regions of the septum lucidum, in front of the anterior commissure, we find the innermost fasciculi of the projection mass where they leave the ganglia only 2 mm. distant from the marginal angle of the hemisphere.

* Vide Plate 49, fig. 10, between A and B.

In regions where the thalamus intervenes, as at the origin of the optic tracts, the lenticular nucleus retiring further outwards makes the distance between the points $5\frac{1}{2}$ mm. In these regions the coronal fibres are distributed chiefly to the upper aspect of the hemisphere and not so exclusively to its marginal angle. Still further back on a plane with the optic radiations to the thalamus, the distance betwixt the same points is $6\frac{1}{2}$ mm., and here the great mass of the projection system no longer runs upwards to the vertex, but immediately upon the emergence from the lenticular nucleus they bend directly backwards towards the occiput and are therefore exhibited as transverse sections of fasciculi (Plate 49, fig. 10, F). A limited supply can still be traced upwards to the cortex of the outer and upper aspect of the hemisphere (Plate 49, fig. 10, A). These facts warrant us in asserting—

1st. In regions anterior to the thalamus the coronal connexions betwixt cortex and motor ganglia with the internal capsule, arise *par excellence* from that marginal aspect of the vertex whose cortex is characterised by the great ganglionic cell formation, and as entering into the composition of FERRIER's motor realm.

2nd. That the median cortex (upper limbic arc) has no connexion with the same ganglia or capsule throughout any of its course.

3rd. That as these ganglia retire outwards before the intervening thalamus, their coronal connexions arise chiefly from the upper and outer aspect of the hemisphere and still further back from the occipital cortex at their own level.

From what has already been stated as regards the distribution of the callosal commissure, it is evident that in the anterior regions of the brain the marginal and exposed aspect adjacent to it will receive a much larger supply of medullated fibres than with the more external aspect, or the cortex of the median aspect, which receives callosal fibres only. In accordance with this a glance at vertical sections of fresh brain shows the dense sheaves of fasciculi which radiate to the marginal angle (Plate 49, fig. 11, E), and the comparative paucity of medullated supply to the limbic arc and outer aspect of hemisphere.

Junction of projection fasciculi with motor ganglia.—The uniform medullary radiations unite into delicate fasciculi which pass between the fibres of the callosal commissure, decussating with them at various angles, and just where they arrive at the surface of the striate ganglion unite into coarser fasciculi and pass into the outer segment of the ganglion, often bending inwards at right angles to their original course (Plate 49, fig. 11, C). The fasciculi thus formed by convergence of the coronal radiations have an average diameter of ·05 mm., but towards the upper pole of the lenticular nucleus large fasciculi are found with a diameter of ·093 mm., much more closely aggregated. At the lowest level of this body they form long delicate bundles (·025 mm. diameter), which pass uninterruptedly after a straight or curved course into its inner segment, whilst midway betwixt these points the fasciculi are far more widely scattered apart and are of medium size (Plate 49, fig. 13, A–B). The delicate bundles traversing the callosal fibres which by their convergence form the

coarse fasciculi of the outer lenticular nucleus are usually one-third or one-fourth the diameter of the latter. Each coarse fasciculus is formed by the union of two or three, and occasionally a large number of such bundles, and during their passage through the outer grey segment frequently divide into two, and appear in their further course through the inner segment subject to still further subdivision. At the upper pole of the lenticular body fasciculi are observed passing from the first segment directly into the internal capsule without previously traversing the inner segment, whilst coronal fasciculi are here also distinctly seen to pass down the internal capsule without establishing any connexion with the ganglia. Upon a plane passing through the anterior or olfactory commissure in horizontal sections of the brain, other fasciculi of medium size, are directed directly backwards into the inner segment of the striate body from the frontal aspect of the caudate nucleus, and obliquely backwards and inwards from its marginal aspects, each fasciculus frequently subdividing on its way but occasionally passing uninterruptedly through the outer segment. In this course they are directed over, beneath, and through the posterior olfactory fasciculus (Plate 49, fig. 9, D). Within the inner segments we meet with two systems of fibres: the coarse fasciculi already dealt with, and a large proportion of minute medullated fibres running separately, and not in fascicles. These ultimate nerve fibres are peculiarly liable to varicosity—they take curved and spiral directions—cross each other frequently, are often much contorted, but are chiefly distributed longitudinally along the course of the large bundles, or in arches across the inner segments of the lenticular nucleus concentric to its base.

They attain a diameter of ·004 to ·005 mm. At a little lower level we find them still more abundantly, but here the orifices of large divided vessels and the peculiar oval nuclei betwixt the coarser bundles indicate that we are examining the anterior perforated space or olfactory area, and now we immediately identify these minute twisted fibres with those already described as peculiar to this region, and can readily trace their connexion with those surrounding the granule layers of the olfactory bulb. At higher levels passing through the anterior end of callosal commissure, coronal radiations pass betwixt cortex of the tip and inner margin of the frontal lobe to the head of the caudate nucleus—the fibres of the corpus callosum crossing their course in their radiations outwards.

To recapitulate—

1. The anterior end of the frontal lobe is connected chiefly with the head of the caudate nucleus.

2. The cortex of the marginal angle at the vertex in front of the thalamus and of a limited surface outside is connected with the centric pole of the lenticular nucleus.

3. The cortex of the outer aspect of the hemisphere behind the latter, and that of the outer aspect of the occipital lobe is connected with that portion of the wedge-shaped nucleus which bends backwards and downwards towards the base.

4. The cortex of the olfactory bulb and lobe is represented in the olfactory area of the nucleus caudatus.

5. The cortex of the inferior limbic lobe will also be strongly represented in the extension of the lenticular nucleus in this direction.

The callosal commissure.—According to the researches of FOVILLE the fibres of the corpus callosum are distributed to none of the convolutions of the brain, but consist of tegmental fibres which, having passed upwards through the thalamus and corpus striatum, unite over these ganglia as a true commissure of the crus cerebri. All my fresh preparations lead me to regard this conclusion as quite fallacious, and demonstrate in the clearest possible manner the passage of the callosal fibres from the convolutions of one hemisphere to those of the other. As maintained by ARNOLD, OELLACHER, and MEYNERT, it is *truly and exclusively a commissure of the hemispheres.* In vertical sections of the brain the following facts I have repeatedly and satisfactorily demonstrated. In sections thus taken through the region of the septum lucidem, the callosal commissure upon entering either hemisphere meets the mass of the projection system obliquely, and decussating and interweaving with this system proceeds along the curved centric pole of the striate body, becoming more and more attenuated as it extends along the lateral aspects of the ganglia, owing to the constant distribution of fibres from its mass to the cortex throughout the whole of this course. In the first part of its course, where it first blends with the projection fibres to the ganglia, a very large proportion of its mass (one-third to one-eighth of the whole) takes a curved course upwards and inwards so as to reach the *median and marginal cortex here* (Plate 49, fig. 12, 6). By far the greater part accompanies the projection fibres, being similarly distributed, viz.: to the cortex of the upper marginal border of the hemisphere and the region just external to it. At this curve of the corpus callosum, where it interweaves with the projection fasciculi prior to their dispersion as coronal radiations, an angular projection is formed which, taking the whole length of the commissure into consideration, really is a prolonged ridge astride which rests the longitudinal fasciculus of the olfactory arcuate system (Plate 49, fig. 12, 7). In vertical sections taken through more posterior planes, it is seen that the portion of the callosal commissure which thus supplies the inner marginal regions of the hemisphere is distinctly to be traced through the whole of its extent as separate from the lower segment which supplies the cortex further outwards. So notably is this the case that all prepared sections show, as a rule, a distinct separation between these two callosal segments, the inner as it were peeling away from the outer—a natural condition due to their opposed direction. It is therefore obvious, at a first glance, that these inner regions of the brain which are similar and identical are connected by the same series of fibres, and the same may readily be maintained for the outer regions of the hemispheres. In fact, the regular superposition of fibres above one another, and the great uniformity of their course in either hemisphere, conclusively show that they unite identical regions of both sides. The most inferior fibres of the callosal commissure are

the lowest throughout their course, and are placed next to the ganglia in their course to the cortex, which for them is the most external part of the hemisphere, *i.e.*, the undermost portion of the corpus callosum terminates in the cortex just above the limbic sulcus externally. On the other hand, the uppermost series of fibres in this commissure connect the more internal aspects of the brain. A superficial section lengthwise through the corpus callosum would therefore deprive the median and inner regions of the brain of their commissural connexions, whilst the *deeper* the incision was carried the more *external* the regions of the hemispheres which would suffer likewise.

Expansion of olfactory arcuate system into occipital cortex.—An important distribution of fibres from the olfactory cortex has been already traced into the occipital lobe lying like a longitudinal fasciculus (of inverted V-shaped form in vertical section) upon the prominent ridge formed by the apposition of the callosal and projection fasciculi (Plate 49, fig. 11, F). The ultimate destination of these fibres may best be studied in vertical sections through the hemisphere behind the posterior commissure. In such sections we expose the central medulla folded around the cornu ammonis, which in its turn lies concentric to the great central ganglia (Plate 49, fig. 10). This mass of central medulla reveals two important regions, (1) the region of section of the great mass of projection fasciculi which here is lateral in position (F); (2) the region of the callosal and arcuate olfactory fasciculi which is median in position (H). The latter with which we are now concerned is wedge-shaped, in such section the base of the wedge directed towards the median cortex, the two converging sides directed outwards. The central core, so to speak, of this wedge is constituted by the callosal fasciculi subdivided into an upper segment destined for the marginal angle and tip of occipital lobe, and a lower segment which is continuous outwards towards the lateral projection system radiating to the cortex throughout this course and the divided fibres of the fornix. Superficial to it and running in the opposite direction is a small band of projection fasciculi, which has also for its ultimate destination the cortex of the outer and upper surface of the hemisphere as far as the marginal angle. Upon the upper basal angle of the wedge rides the fasciculus of the olfactory arcuate and arcuate system of the upper limbic arc, which here have accumulated into a vast collection of fibres opposed to the whole base and upper side of the wedge. These fibres, however, are no longer found in transverse section, but are seen spreading extensively on all sides to the cortex (1) of the median aspect (upper limbic arc), (2) the marginal angle of the hemisphere, and (3) the cortex of the vault as far outwards as the superior parietal sulcus. Outside the latter sulcus the coronal distribution to the cortex consists of scanty projection and callosal fasciculi; within the sulcus, on the other hand, the cortex is supplied by dense callosal, a few projection fasciculi, and the notably large supply of olfactory and limbic arcuate fibres. This rich medullated region reveals its wealth of medullated fibres compared with the rest of the hemisphere when simply examined by the naked eye, and in osmic acid preparations shows the same in

the far deeper staining which it takes. The olfactory arcuate fasciculi therefore are wholly distributed to that portion of the median and superficial cortex of the occipital lobe which is characterised by the granule cell formation which here forms a deep second layer (Plate 49, fig. 1, K, D). This formation has been already fully described under the name of the modified upper limbic type. This region is moreover characterised by a further peculiarity, viz.: the two intra-cortical arcuate bands. The more superficial of these is a broad streak of medullated fibres which arising from the apical processes of the large cells in the cornu ammonis, as its first layer (nuclear—MEYNERT) is continued along the lower half of the first cortical layer of the upper limbic arc, and bending over on to the upper surface of the hemisphere is almost immediately lost here. Beneath it lies a second shallower medullated band a little over half the depth of the former, and separated from it by the second layer of granule cells. This stripe also arises from the cornu ammonis, and likewise running parallel to the cortex terminates even earlier than the more superficial stripe, as it ends abruptly at the upper marginal angle of the hemisphere. In such as we are now dealing with (fresh vertical sections), both these stripes may readily be seen by a hand lens running as delicate white streaks parallel to the surface of the cortex of the upper limbic arc, being lost beyond the upper marginal angle, whence no similar white streak can be detected until we arrive opposite the great mass of the projection system which here takes a lateral position. Here again we observe a delicate medullated stripe in the first cortical layer running towards the limbic sulcus, but lost prior to its arrival at that spot. This stripe is even shallower than the deeper arcuate stripe in the upper limbic arc.

Region of expansion of central olfactory fasciculus.—It will be remembered that the termination posteriorly of the inferior limbic arc is characterised by the large size of the nerve-cells of its second cortical layer—the *modified olfactory type.* If *horizontal* sections of the occipital end of the frozen brain be carried through this region, the following facts may be readily confirmed. Most internally is the curved border of the cornu ammonis; next to it comes the granule region, extended from the upper limbic arc; still further outwards is the peculiar region alluded to; and beyond its boundary (the limbic sulcus) is the curved surface of the extra-limbic portion of the hemisphere.

To the *naked eye* a great dissimilarity is at once observed betwixt the appearance of the extra-limbic and the limbic portion. The former exhibits a medulla which has a slight translucent aspect and is of a pale tint, but markedly contrasted with the *perfectly opaque and brilliant white colour* of the limbic medulla. The line of demarcation, again, betwixt these two is sharp and abrupt, and extends from the depths of the corpus callosum directly outwards to the limbic sulcus. Microscopic examination clearly shows this difference in colour to be due to the *vast preponderance* of medullated nerve-fibres in the limbic region at this site, which radiate outwards to the cortex from the terminal portion of the callosal commissure. In the extra-limbic portion of the

hemisphere we likewise observe medullated fibres which radiate outwards to the cortex along its whole extent, and proceeding solely from the corpus callosum do not form such dense aggregations, but light radiating fibres some distance apart. In the limbic portion, however, the same fibres are present, plus a strong reinforcement from the posterior extensions of the anterior commissure, *i.e.*, the central olfactory fasciculus. Here then appears demonstrated an important fact, that the cortex of the modified olfactory type (Plate 49, fig. 1, T to W), receives medullated radiations so extremely rich in fibres that it is mapped out to the naked eye from the neighbouring extra limbic medulla by its notable white brilliant aspect, and that these fibres include the terminal expansion of the central olfactory fasciculus.

Here again we meet with *two intra-cortical arciform stripes* of medulla disposed as in the modified upper limbic arc, viz.:—

(*a*) A superficial streak at the lowest confines of the first layer.

(*b*) A deeper streak beneath the large swollen cells of second layer.*

The superficial stripe is, however, here the shallower of the two, and the deeper stripe attains a width equal to the first band in the upper limbic arc. In *horizontal sections* the medullated fibres of these two streaks will be divided obliquely. In sections such as I have just been considering a rich series of arcuate fibres will also be found extending backwards through the *extra-limbic lobe* from the anterior realms of the brain, which thin out gradually towards the abrupt line of denser medulla, commencing at the limbic sulcus, and wholly disappear here. This is the arcuate system of the extra-limbic medulla.

The above facts enable me to conclude that at the occipital pole of the hemisphere there are two important regions definitely mapped out by coarse external configuration of the brain and also by minute structural divergences.

These regions are histologically distinguished by the possession of a cortex, which is peculiar to each, and which we have named respectively the modified upper and lower limbic types. Each region is associated with that of the opposite hemisphere by the callosal commissure.

Each region is brought into relationship with the olfactory lobe and bulb; the upper limbic by means of the arcuate olfactory, the lower limbic through the medium of the central olfactory fasciculi after the decussation in the posterior commissure.

Each region is moreover supplied with the peculiar double stripe of medullated fibres, forming arcuate systems within the cortex itself.

Hence we have in these regions a reflection backwards of the olfactory sensory surface brought strongly into association with the cornu ammonis by means of the arcuate intra-cortical stripes.

* The site of these intra-cortical bands of medulla is approximately given in Plate 50, fig. 6, *a* and *b*.

DEPTH of Cortical Layers on a Plane with Genu of Corpus Callosum.

	Gyrus fornicatus.	Sagittal angle.	Extra-limbic.	Near limbic sulcus.
	mm.	mm.	mm.	mm.
First layer	·372	·372	·348	·279
Small pyramids . .	·604	·744	1·023	·558
Granule belt . . .	..	..	·372	..
Ganglionic belt . .	·232	·232	·186	·408
Spindle cells . . .	·511	·883	·883	1·069

DEPTH of Cortical Layers on a Plane with posterior border of Corpus Callosum.

	Gyrus fornicatus.	Sagittal angle.		Extra-limbic.
	mm.	mm.		mm.
Peripheral zone . .	·441	·325		·372
Granule layer . .	·418	·372	Small pyramids	·372
			Granules . .	·372
Ganglionic layer . .	·465	·604		·604
Spindle cells . . .	·372	·604		·744

DEPTH of Cortical Layers of the Modified Lower Limbic Type. (Rabbit.)

	mm.
Peripheral cortical zone	·279
Inflated cell formation	·883
Ganglionic layer	·372
Pale belt.	·279
Spindle cells	·418 to ·655

DEPTH of Cortical Layers in the Cornu Ammonis. (Rabbit.)

	Peripheral zone.	Striate and lacunar layers.	Ganglionic cells.	Molecular layer.	Medullated layer.
	mm.	mm.	mm.	mm.	mm.
Anterior regions	·325	·930	·093	·523	·395
Average at six different sites.	·424	·915	·112	·397	·385

Average depth of whole cortex of ammon's horn =2·233 mm.

Dimensions of Nerve-cells in Brain of Rabbits.

Upper Limbic Arc.

	Second layer of small pyramids.		Ganglionic layer.	
Near frontal pole	$17\mu \times 11\mu$	Nucleus 9μ	$24\mu \times 17\mu$	$N=10\mu$
In front of corpus callosum	$17\mu \times 12\mu$	$N=9\mu$	$24\mu \times 17\mu$	$N=13\mu$
Anterior regions of ,,	$15\mu \times 13\mu$	$N=8\mu$	$32\mu \times 18\mu$	$N=13\mu$
Posterior regions of ,,	$16\mu \times 11\mu$	$N=8\mu$	$27\mu \times 16\mu$	$N=13\mu$
Behind corpus callosum	$13\mu \times 9\mu$	$N=8\mu$	$26\mu \times 16\mu$	$N=13\mu$

Granule cells $=10\mu \times 8\mu$ $N=5\mu$.

Gyrus Hippocampi.

Pyramidal cells.		Fusiform ganglionic.	
$19\mu \times 12\mu$	$N=9\mu$	$31\mu \times 13\mu$	$N=13\mu$

Modified Lower Limbic Cortex.

	Second layer of inflated cells.		Third or pyramidal cells.	
From different sites	$37\mu \times 32\mu$	$N=13\mu$	$23\mu \times 13\mu$	$N=13\mu$
	$37\mu \times 23\mu$	$N=13\mu$		
	$46\mu \times 27\mu$	$N=13\mu$		

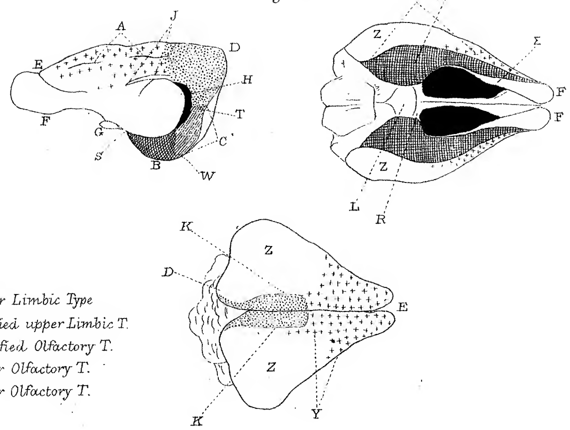
Outer Olfactory Cortex.

	Second layer.		Ganglionic layer.	
Distant from bulbus olfactorius	$19\mu \times 12\mu$	$N=9\mu$	$31\mu \times 13\mu$	$N=13\mu$
,, ,, ,,	$18\mu \times 10\mu$	$N=9\mu$		
Beneath bulbus olfactorius	$17\mu \times 11\mu$	$N=9\mu$		

Extra-Limbic or Parietal Cortex.

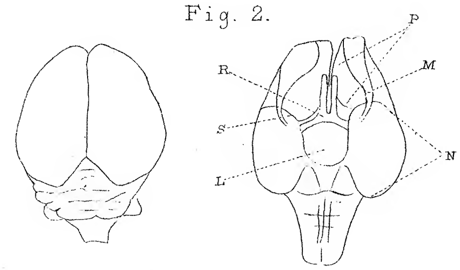
	Second layer.			Ganglionic layer.	
In front of corpus callosum	$22\mu \times 12\mu$	$N=9\mu$		$32\mu \times 16\mu$	$N=13\mu$
Anterior regions of ,,	$21\mu \times 13\mu$	$N=9\mu$		$32\mu \times 16\mu$	$N=12\mu$
Posterior regions of ,,	$17\mu \times 10\mu$	$N=8\mu$	Largest	$60\mu \times 18\mu$	$N=13\mu$
				$31\mu \times 16\mu$	$N=12\mu$
Behind corpus callosum	$13\mu \times 11\mu$	$N=8\mu$		$24\mu \times 18\mu$	$N=12\mu$
Close to occipital pole	$20\mu \times 11\mu$	$N=9\mu$		$31\mu \times 19\mu$	$N=13\mu$

Fig. 1.



++++ *Upper Limbic Type*
Modified upper Limbic T.
Modified Olfactory T.
Outer Olfactory T.
Inner Olfactory T.

Fig. 2.



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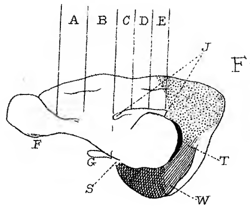

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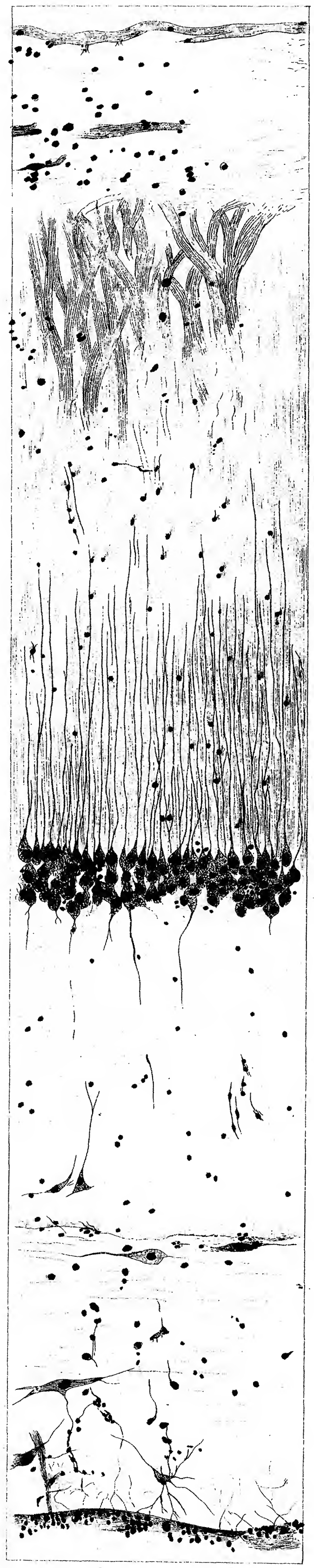

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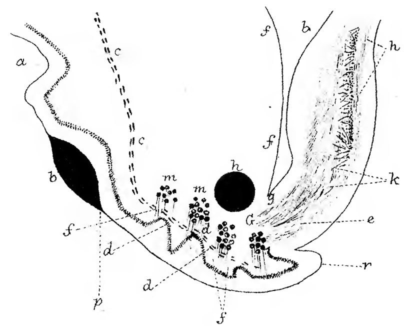

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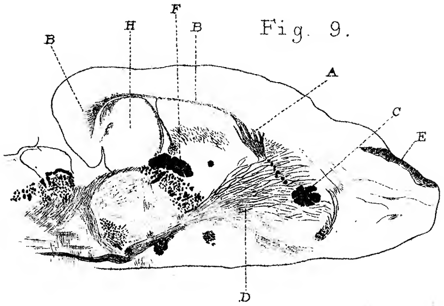

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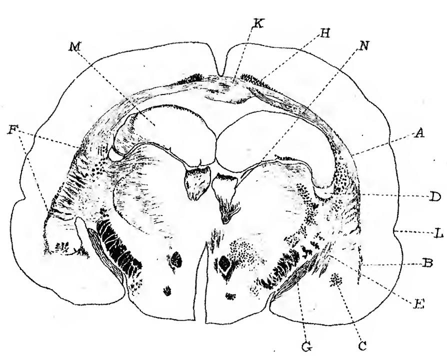
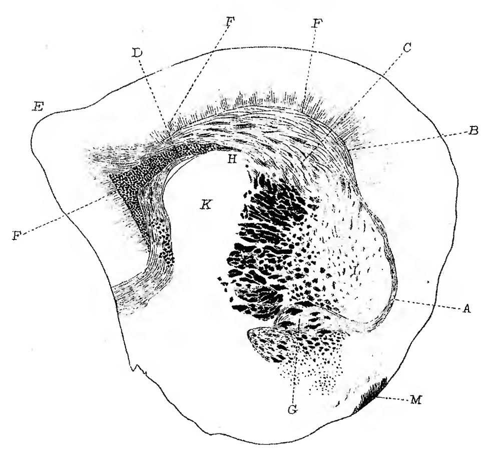


Fig. 11.



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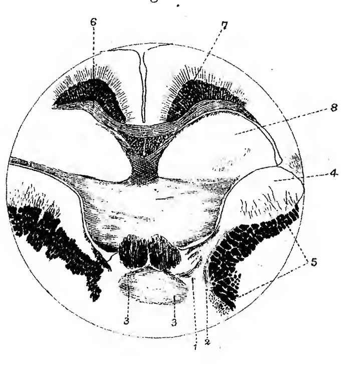

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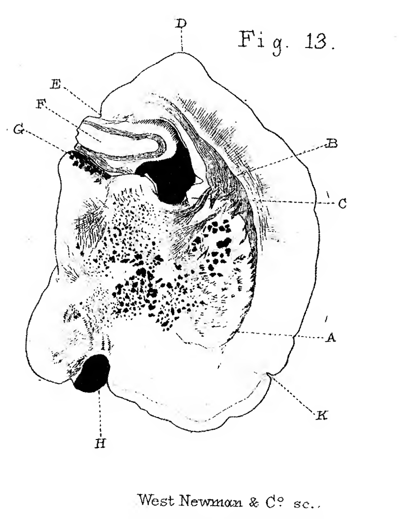

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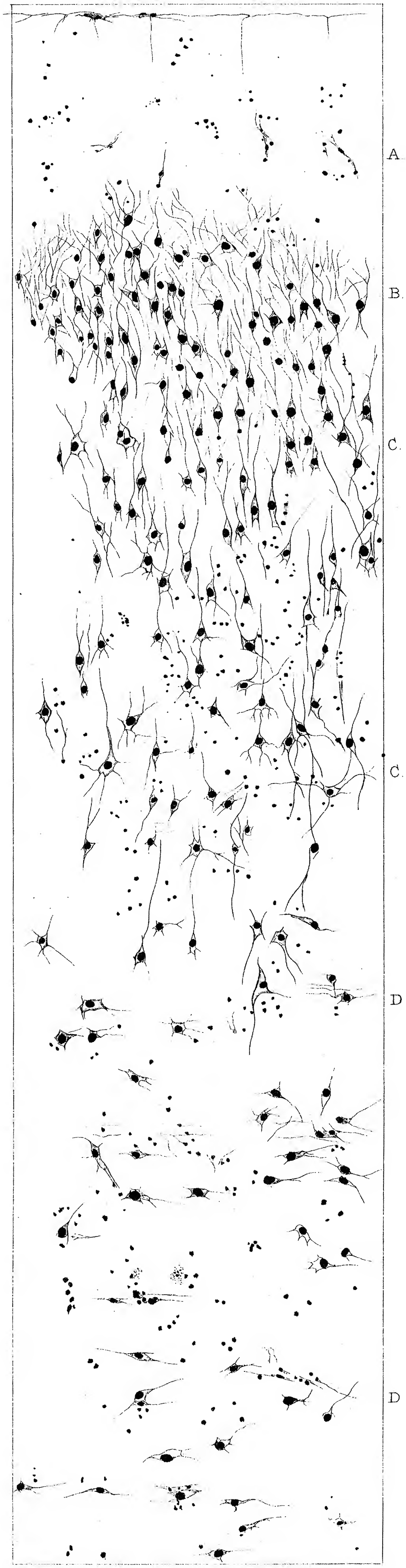

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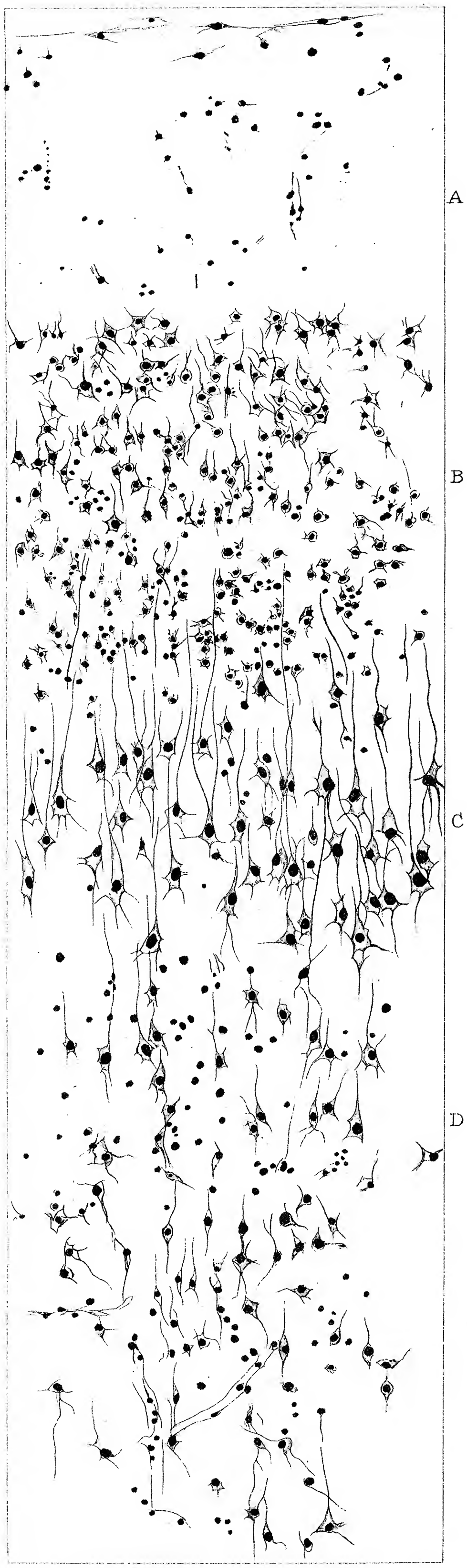

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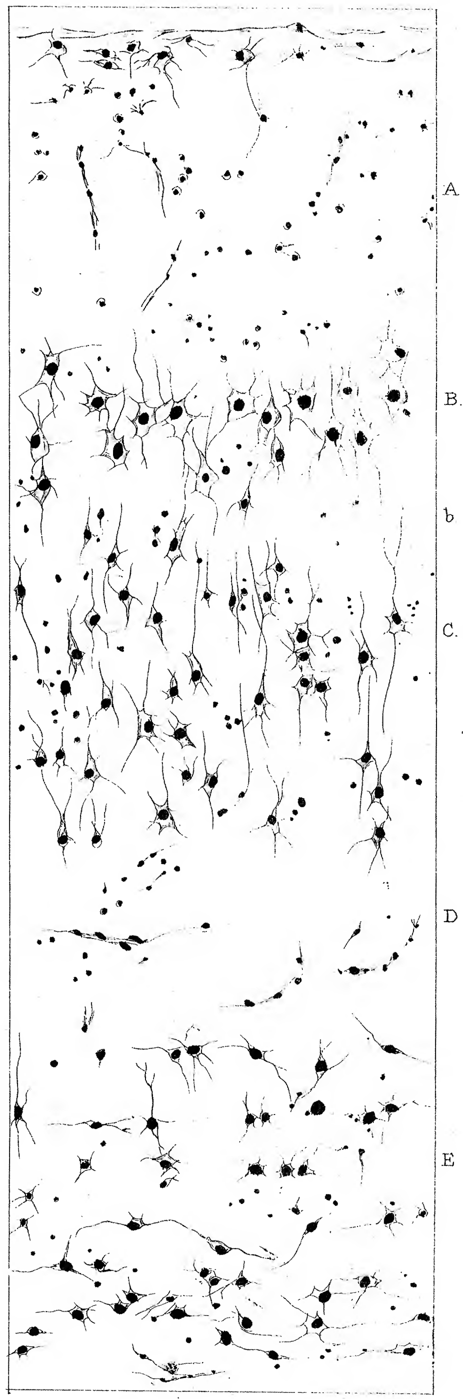

Fig 1

Fig 2

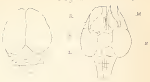

Fig 3

Fig 8

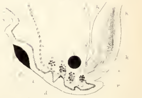

Fig 9

Fig 11

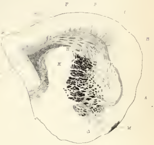

Fig 10

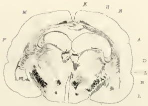

Fig 12

Fig 13